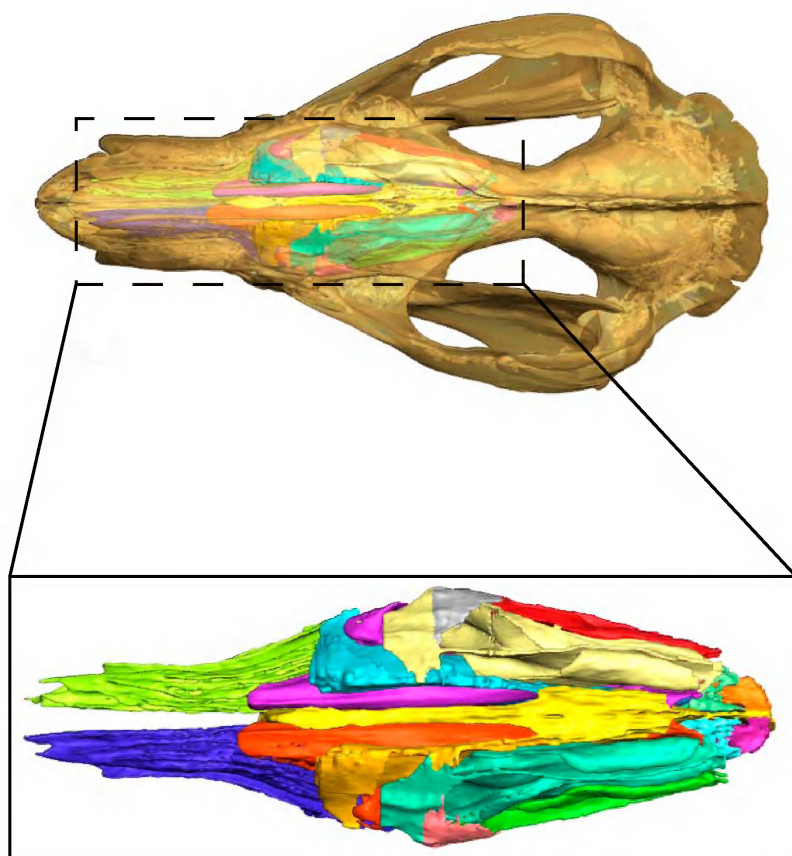

COMPARATIVE MORPHOLOGY OF THE INTERNAL NASAL SKELETON OF ADULT MARSUPIALS BASED ON X-RAY COMPUTED TOMOGRAPHY

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

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CONTENTS

Abstract	3
Introduction	3
Phylogenetic Hypotheses for Relationships within Marsupialia	4
Marsupial Nasal Cavity.	7
Goals of This Paper	8
Institutional Abbreviations	8
Materials and Methods.	8
Specimens Examined.	8
CT Imaging	8
Anatomical Terminology.	9
Phylogenetic Character Matrix.	9
Description	11
Osteology of Nasal Cavity as a Whole in Adult Marsupials	11
Cartilaginous Elements of Adult Marsupials	15
Maxilloturbinal.	18
Nasoturbinal	18
Endoturbinals.	20
Ectoturbinals	24
Posterior Transverse Lamina	26
Cribriform Plate	28
Ossified Nasal Septum.	31
Frontal Recess/Sinus	31
Maxillary Recess/Sinus	33
Taxonomic Variation from Generalized Marsupial Condition	34
Intraspecific Variation.	64
Quantitative Data	67
Discussion	67
Character Distributions	67
Ancestral Reconstruction of Number of Turbinals.	70
Comparisons of Turbinals with Ecological Characteristics	74
Conclusions	75
Acknowledgments	77
References	77
Appendix 1: Terminology for Osteological Structures Described from Adult Skulls.	83
Appendix 2: Character List from the Internal Nasal Skeleton.	88
Appendix 3: Taxon Character Matrix for Characters from the Internal Nasal Skeleton.	91

ABSTRACT

The internal skeleton of the nasal cavity is sporadically and often incompletely described for many marsupial species and mammals in general. Here, I provide an anatomical survey of the ethmoid in the skulls of adult marsupials based on examination of computed tomography (CT) imagery of 29 taxa representing all the major extant groups of marsupials. This survey resulted in a description of the “generalized condition” for the morphology of the marsupial ethmoid bone, ossified nasal septum, and associated structures of the interior of the nasal cavity. I also described how the ethmoid in different clades varies in morphology from the general condition for Marsupialia. Intraspecific variation of the ethmoid was described based on a sample of 18 specimens of *Monodelphis domestica*, the gray short-tailed opossum, and asymmetries within a single specimen are documented for other taxa. For the most part I follow the nomenclature of previous nasal cavity workers, but I also provide explicit definitions of all the terms used and some of the common synonyms for these in the literature. Endoturbinals and ectoturbinals are numbered sequentially following the work of previous authors, because of the issues with serial homology for these elements.

The number of elements of the marsupial ethmoid is fairly conserved with the typical and likely ancestral condition being the presence of an ossified maxilloturbinal, nasoturbinal, two ectoturbinals, and five endoturbinals. However, there is considerable variation in the complexity, spatial placement, and overall morphology of the bony internal skeleton of the nose. Based on this descriptive work, I documented 35 discrete characters from the ethmoid and ossified nasal septum complex in marsupials. These characters were scored for this sample of marsupials and five mammalian outgroups. Examination of these characters on preexisting topologies of marsupial relationships revealed some phylogenetic signal for this sample of marsupial species. Three of the characters are punitively diagnostic for previously recognized clades within Marsupialia. It is possible that when this matrix is combined with morphological data from other anatomical systems and molecular data that previously unrecognized or controversial clades within Marsupialia may be supported. Even so, the relatively little amount of phylogenetic signal from my character matrix prompted me to search for alternative explanations for mechanisms driving the variation in this anatomical system. Consequently, I compared ecological data with the number of ecto- and endoturbinals as a preliminary test to determine whether some of the interspecific variation in the osteology of the ethmoid is a result of ecological factors, but found few correlations to support this idea.

Finally, my study highlights some issues with homologies of mammalian nasal cavity elements that need to be resolved and reexamined. These include whether the ossified nasal septum arises from the presphenoid or the mesethmoid, and a test of the current view of serial homology of the endoturbinals and ectoturbinals.

INTRODUCTION

Marsupials are an ecologically and morphologically diverse group of mammals with over 330 extant species (Wilson and Reeder, 2005) that includes charismatic and familiar animals such as the koala, sugar glider, kangaroos, and opossums. Extant marsupials are found in terrestrial, arboreal, semiaquatic, and fossorial ecological niches. They employ many locomotory patterns to move around in their habitats such as scansoriality, saltatoriality, and gliding.

Marsupials belong to the clade Marsupialia, which is defined as a crown group (following

de Queiroz and Gauthier, 1990), such that it includes the most recent common ancestor of extant marsupials and all descendants of that ancestor (sensu Rougier et al., 1998; Flynn and Wyss, 1999). Placentalia is the crown sister clade to Marsupialia, both being united in the clade Theria. Metatheria is a stem-based name referring to the clade containing all therian mammals that are more closely related to Marsupialia, including marsupials, than to Placentalia (sensu Rougier et al., 1998; Flynn and Wyss, 1999). Metatheria contains a number of fossil mammals that resemble marsupials in some characteristics but are excluded from the crown group.

When comparing only extant mammals, living marsupials are distinguished by their mode of reproduction, which entails a short gestation period, altricial young born live as opposed to hatching from an egg as in monotremes, and an extended lactation period, typically occurring in a pouch. Although marsupials are often informally called the “pouched mammals,” the females of only about half of extant species have some sort of a pouch or marsupium (Vaughan et al., 2000).

Extant marsupials are characterized by a number of other morphological features, but few of these are synapomorphies for Marsupialia (see summary in Kielan-Jaworowska et al., 2004). These include reproductive, other soft tissue, skull, and postcranial skeletal characters. Some of the more informative characters on the skull pertain to the ear region, and in particular the petrosal (Wible, 1990; Rougier et al., 1998). In addition, a dental replacement pattern of only P3/p3 is present in extant marsupials as well as some nonmarsupial metatherians (Cifelli et al., 1996; Cifelli and de Muizon, 1998; Rougier et al., 1998), indicating that this character is an apomorphy for a more inclusive clade than crown Marsupialia.

Phylogenetic Hypotheses for Relationships within Marsupialia

As the crown sister clade to placental mammals, and because of their unique reproductive biology, marsupials are the focus of intense research in a wide range of disciplines including biomedicine, genomics, biogeography, ecology, biomechanics, behavior, physiology, and paleontology (e.g., Hinds and Saunders, 1997; Tyndale-Biscoe, 2005; Armata et al., 2006). Although testing relevant hypotheses in many of these fields requires an understanding of evolutionary relationships, many aspects of marsupial phylogeny remain enigmatic despite recent advances involving analyses of both morphological and molecular data (e.g., Springer et al., 1997; Burk et al., 1999; Colgan, 1999; Jansa and Voss, 2000; Amrine-Madsen et al., 2003; Horovitz and Sánchez-Villagra, 2003; Voss and Jansa, 2003, 2009; Asher et al., 2004; Cardillo et al., 2004; Nilsson, 2004;

Jansa et al., 2006; Sánchez-Villagra et al., 2007; Beck, 2008; Meredith et al., 2008). The major areas of conflict in marsupial phylogeny involve: the placement of *Dromiciops gliroides*, the only extant member of the South American group Microbiotheriidae, within Australiadelphia (the least inclusive clade containing *Dromiciops* and all extant Australasian groups); relationships between *Notoryctes*, Dasyuromorphia, and Peramelemorphia; and higher relationships within Diprotodontia.

Some recent analyses of nuclear and mitochondrial genes found *Dromiciops* to be the sister taxon to a monophyletic Australasian clade (Amrine-Madsen et al., 2003; Beck, 2008; Meredith et al., 2008; fig. 1). Other analyses found *Dromiciops* nested within the Australasian radiation, either as the sister taxon to Diprotodontia (e.g., Horovitz and Sánchez-Villagra, 2003; Cardillo et al., 2004; Sánchez-Villagra et al., 2007; fig. 2), or as the sister taxon to a clade that is more inclusive than Diprotodontia (e.g., Springer et al., 1997; Asher et al., 2004).

The relationships between *Notoryctes*, Dasyuromorphia, and Peramelemorphia (bandicoots and bilbies) are also unresolved. Some analyses based on nuclear and mitochondrial genes found *Notoryctes* to be the sister taxon to Dasyuromorphia with Peramelemorphia the sister taxon to that clade (e.g., Amrine-Madsen et al., 2003; Beck, 2008; Meredith et al., 2008; fig. 1). Other trees based on DNA (Springer et al., 1997) and combined morphological and DNA data (Asher et al., 2004) recovered the *Notoryctes* + Dasyuromorphia clade but not the more inclusive clade containing Peramelemorphia. Some morphological analyses found *Notoryctes* to be the sister taxon to Peramelemorphia, but did not recover a more inclusive clade consisting of only *Notoryctes*, Peramelemorphia, and Dasyuromorphia (e.g., Horovitz and Sánchez-Villagra, 2003; Sánchez-Villagra et al., 2007; fig. 2).

There is also considerable conflict between higher relationships within Diprotodontia. One clade that is consistently recovered by both molecular and morphological data is Vombatiformes (Phascolarctidae + Vombatidae); however, the relationship of this clade to other diprotodonts is unresolved. Some

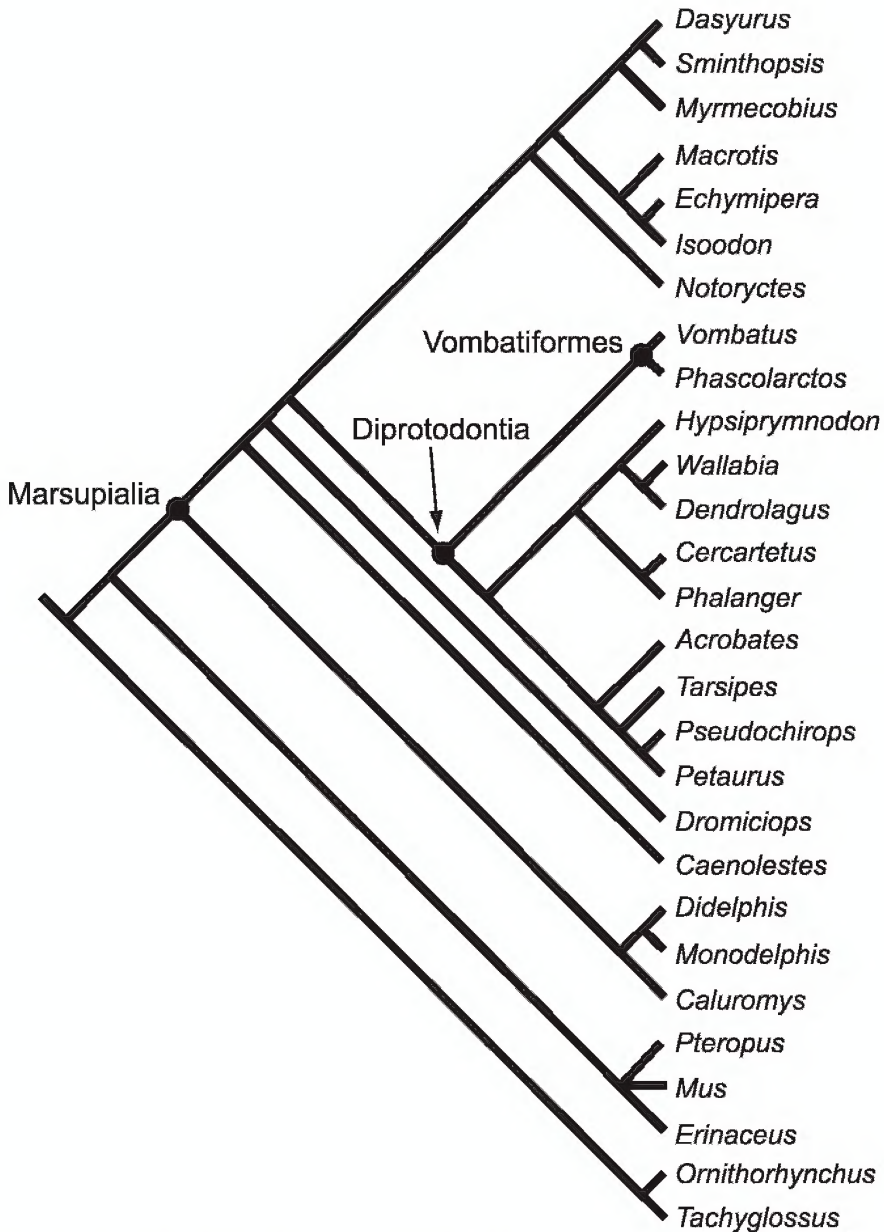


Fig. 1. Modified topology from Meredith et al. (2009) based on Bayesian analysis of five nuclear genes. Taxa for which I do not have nasal cavity data were pruned from the topology or if possible substituted for closely related species for which I do have nasal cavity data. *Didelphis* was used as a representative of Didelphinae; *Dendrolagus* was substituted for *Aepyprymnus*; *Wallabia* was substituted for *Macropus*; *Sminthopsis* was substituted for *Phascolosorex*. Substitutions within Marsupialia were based on the topologies by Cardillo et al. (2004). The outgroups were pruned from the topology of Meredith et al. (2009) and instead the following taxa for which I have nasal cavity data were included: *Mus*, *Pteropus*, *Erinaceus*, *Ornithorhynchus*, and *Tachyglossus*. The polytomy for the placental mammals reflects the uncertainty in higher level systematics for Placentalia, whereas the monotreme relationships are well established (e.g., Rowe et al., 2008).

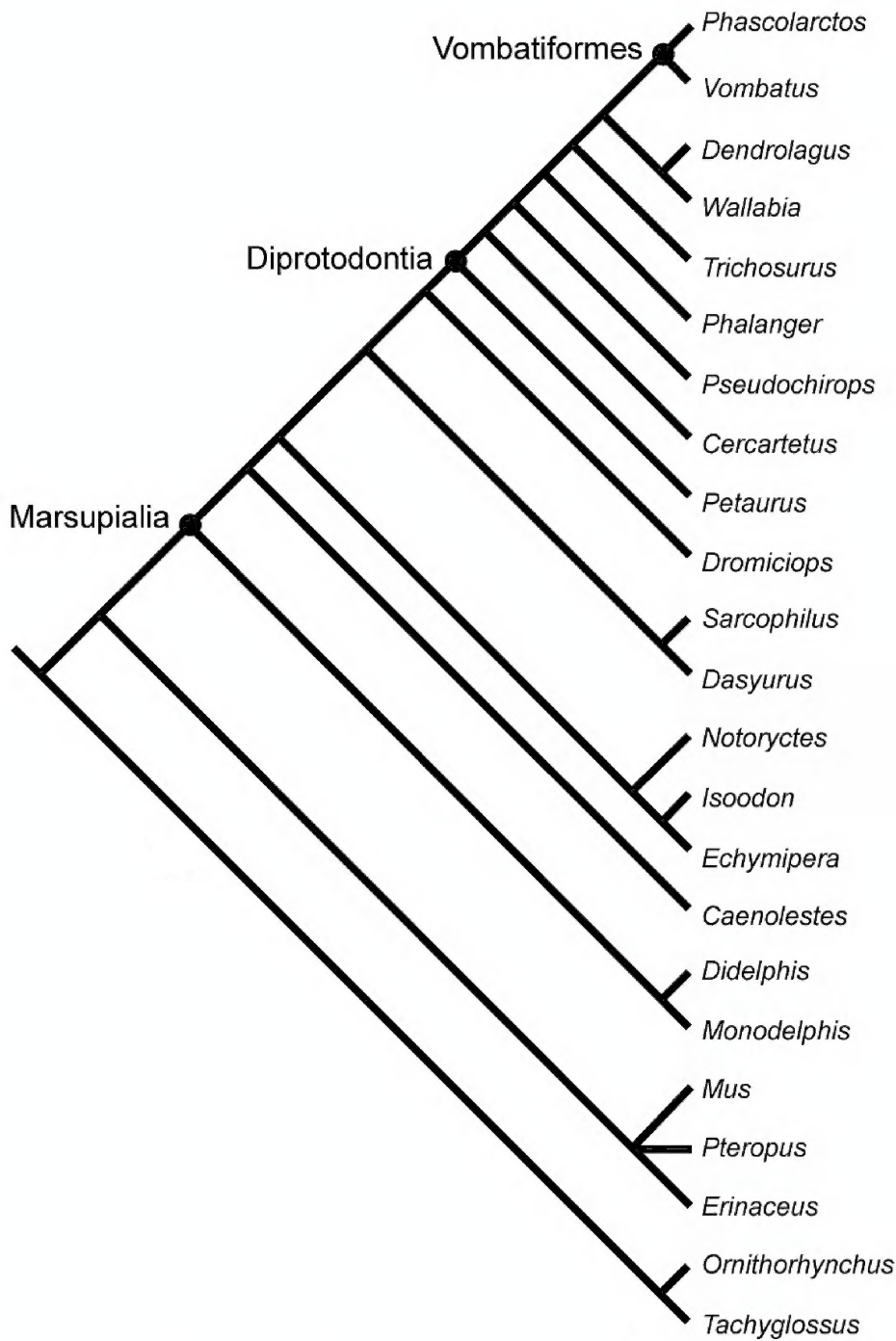


Fig. 2. Modified strict consensus tree from Sánchez-Villagra et al. (2007) based on morphological data. Taxa for which I do not have nasal cavity data were pruned from the topology or if possible substituted for closely related species for which I do have nasal cavity data. *Wallabia* was substituted for *Macropus*; *Sarcophilus* was substituted for *Dasyuroides*; *Isoodon* was substituted for *Perameles*. Substitutions within Marsupialia were based on the topologies by Cardillo et al. (2004). For explanation of outgroups used, see caption for figure 1.

analyses based solely on DNA data found Vombatiformes as the sister taxon to all other diprotodonts (e.g., Amrine-Madsen et al., 2003; Beck, 2008; Meredith et al., 2008; fig. 1), whereas morphological analyses nested Vombatiformes more deeply in Diprotodontia as the sister taxon to Macropodidae (e.g., Horovitz and Sánchez-Villagra, 2003; Sánchez-Villagra et al., 2007; fig. 2). Relationships between the other major groups of diprotodonts are also largely unresolved and the monophyly of some family-level clades are questionable (e.g., Phalangeridae; Horovitz and Sánchez-Villagra, 2003; Sánchez-Villagra et al., 2007).

Marsupial Nasal Cavity

The nasal skeleton and associated soft tissue structures and cavities are not documented for many mammalian taxa, mainly because of the difficulty in visualizing this anatomy. Increased use of computed tomography (CT) technology has allowed for more detailed studies of the nasal and associated cavities (e.g., Rowe et al., 2005; Rossie, 2006), as is apparent by an entire issue of *The Anatomical Record* devoted to the study of paranasal sinuses (Laitman and Albertine, 2008). Even so, very few characters from the nasal cavity are incorporated in phylogenetic analyses (but see Rowe, 1988; Freyer, 1999; Sánchez-Villagra, 2001; Luo et al., 2007; Rossie, 2008; Stöbel et al., 2010). The mammalian nasal skeleton, especially the ethmoid and its constituent turbinals, has an elaborate morphology that potentially may provide many new phylogenetic characters. Previous studies based on laborious and destructive methods (e.g., Allen, 1882; Paulli, 1900a, 1900b, 1900c; Negus, 1958) show that the number and complexity of the internal nasal skeleton elements certainly varies between taxa.

Below I summarize some of the more salient studies on the nasal cavity of marsupials. The published descriptions of the nasal cavities of marsupials either examined the internal nasal skeleton of adults or are based on serial sections of pouch young and hence examine only the cartilaginous precursors to the bony elements. Few studies combined both approaches.

One of the earliest descriptions of the marsupial internal nasal skeleton came from

Paulli (1900a) who described the ossified turbinal elements in adult specimens of *Didelphis virginiana*, *Dasyurus viverrinus*, *Phascogale larctos cinereus*, *Petrogale penicillata*, *Macropus robustus*, *M. rufogriseus*, and *Trichosurus vulpecula*. The main contribution of this study was a count of the number and types of turbinal elements in these taxa.

The chondrocrania of a number of marsupials were described in the early part of the 20th century. The vomeronasal organ and surrounding cartilaginous structures of *Notoryctes typhlops* were described based on serial sections by Sweet (1904); however, no mention is made about the turbinal elements. The chondrocranium of *Perameles* was described by Cords (1915) and Esdaile (1916). Esdaile (1916) examined serial sections of six individuals of various sizes representing two different species of *Perameles* (*P. obesula* and *P. nasuta*) at multiple stages of development. The description follows the development of the turbinals, among other elements of the *cavum nasi*, in these stages. The chondrocranium of *Didelphis marsupialis* was described by Toeplitz (1920), including the turbinals. A description of the chondrocranium of *Caluromys philander* based on transverse serial sections of two individuals was published by Denison and Terry (1921).

Unpublished German theses and dissertations also describe the nasal cavity in some marsupials. The ethmoid region of the chondrocranium of *Wallabia rufogrisea* was described in an unpublished dissertation by Müller (1986). The chondrocranium of *Vombatus ursinus* was described by Klutznny (1994) based on two different-sized pouch young. Perhaps the most significant unpublished description of the ethmoidal region of a marsupial is by Freyer (1999) based on serial sections of pouch young and adult specimens of *Monodelphis domestica*. This thesis describes the order of appearance of the different cartilaginous elements that eventually ossify to form turbinals in *M. domestica* compared to *Didelphis marsupialis* and *Thylacinus cynocephalus*. In addition, Freyer (1999) presents a matrix of 38 characters on the development of the ethmoidal region of the chondrocranium for several marsupial taxa scored from the literature and based on personal observations.

The internal nasal skeletons of adults were described for *Caenolestes obscurus* (Osgood, 1921) and *Dasyercus cristicauda* (Wood Jones, 1949). These descriptions are mainly based on hemisectioned skulls and mostly rely on previous publications for comparative material.

The bony nasal cavity and associated soft tissue structures, particularly the vomeronasal organ and the distribution of different types of epithelia, were described for *Isodon macrourus* (Kratzing, 1978), *Tarsipes rostratus* (Kratzing, 1982), and *Phascolarctos cinereus* (Kratzing, 1984) based on serial sections of heads of adult specimens.

Sánchez-Villagra (2001) described the ontogeny and phylogeny of the vomeronasal complex in marsupials and summarized previous work in this area. This work resulted in 16 morphological characters that were scored across almost all of the major clades of marsupials (except Notoryctidae).

The ethmoid, ossified nasal septum, and associated nasal recesses were described from skeletal specimens of *Monodelphis domestica* using computed tomography (CT) imagery of skulls (Rowe et al., 2005). This study is unique for providing the first description of the nasal cavity of a marsupial based on CT imagery, for providing measurements of surface areas and volumes of nasal passageways, and for discussing the ethmoid as a compound element comprising the maxilloturbinal, nasoturbinal, endoturbinals, and ectoturbinals. The paper by Rowe et al. (2005) laid a foundation for this survey on the ethmoid in extant marsupials.

Goals of this Paper

There are two main goals of this paper. The first is to present an anatomical survey of the internal nasal skeleton of adult marsupials based on CT imagery from representatives of all major extant clades. The second goal is to examine data from this anatomical region of marsupials in a comparative framework to determine the phylogenetic utility of this portion of the skull.

Institutional Abbreviations

AMNH, American Museum of Natural History, Department of Mammalogy, New

York, New York; **FMNH**, Field Museum, Department of Zoology, Division of Mammals, Chicago, Illinois; **KU**, University of Kansas, Natural History Museum, Division of Mammalogy, Lawrence, Kansas; **TMM M**, extant mammal collections of the Texas Natural Science Center housed at the Vertebrate Paleontology Laboratory, Austin, Texas; **TR pers. collect.**, personal collections of Timothy Rowe of the Jackson School of Geosciences, the University of Texas at Austin; **USNM**, Smithsonian National Museum of Natural History, Department of Vertebrate Zoology, Division of Mammals, Washington, D.C.; **UTCT**, University of Texas High-Resolution X-ray Computed Tomography Facility, Austin, Texas.

MATERIALS AND METHODS

Specimens Examined

Exemplars of all the major extant clades of marsupials (following the phylogenies of Springer et al., 1997; Amrine-Madsen et al., 2003; Asher et al., 2004; Sánchez-Villagra et al., 2007) are represented in this study (see table 1 for specimen list). I also examined individuals of a growth series of *Monodelphis domestica*, the gray short-tailed opossum. This sample consists of 18 opossums ranging in age from 27 days old to breeding adults (Macrini et al., 2007b). A handful of extant placental and monotreme taxa were also examined for outgroup comparison; these specimens are listed in table 1. Most of the specimens examined are dry skulls, but other types of preparations, such as fresh dead and ethanol-preserved specimens, were also included in this analysis.

CT Imaging

All of the specimens examined here (table 1) were imaged using high resolution X-ray computed tomography (HRXCT) at the UTCT. Details about HRXCT are provided in a number of other sources (e.g., Rowe et al., 1997; Carlson et al., 2003). Nearly all the specimens were scanned in their entirety through the coronal (transverse of some authors) slice plane, although sagittal and horizontal planes were also available for study

through digital “reslicing” of the specimens (see Kearney et al., 2005; Maisano and Rieppel, 2007, for examples of techniques). The names of anatomical planes used here are those typically applied for nonprimate vertebrates, and some usages may differ with anatomical terminology used explicitly for humans and other hominids. For example, the transverse plane of human anatomical nomenclature is synonymous with the horizontal plane as used in this paper.

Digital renderings of various turbinates were isolated from CT images using Amira 4.0 (2005, Mercury Computer Systems; www.tgs.com), a program designed for the manipulation and visualization of voxel data. Techniques for extraction of bony elements from CT images are described in detail by others (e.g., Bever et al., 2005; Kearney et al., 2005; Maisano and Rieppel, 2007). The general principals and protocols follow for segmentation of elements in Amira.

Throughout the description, references are made to specific CT images for a particular taxon. The prefix C is used to designate an image from the coronal plane, and consecutive CT images are rendered with a dash (e.g., C100–102). CT images and derivative animations are visible on the Digimorph website (table 2).

Anatomical Terminology

Following the literature, the ethmoid was studied using two different approaches, one that examines only adult specimens (e.g., Allen, 1882; Paulli, 1900a, 1900b, 1900c) and another that concentrates on comparative development of the nasal capsule (e.g., Voit, 1909; Maier, 1993a, 2000). However, these two approaches are not necessarily mutually exclusive, as data from both chondrocrania and adult skulls can be incorporated in the same analysis (e.g., Rowe et al., 2005; Rossie, 2006).

It is true that all stages of development should be studied when considering the evolutionary relationships of organisms (Maier, 1993a). However, growth series showing comparative development are not assembled for many extant vertebrate species, and certainly not for all the marsupial species examined in this paper. In addition, very few fossil vertebrate taxa are known from growth series or from specimens preserving early

stages of craniogenesis. Furthermore, cartilaginous portions of the skull rarely fossilize, making it nearly impossible to directly compare the chondrocrania of fossil taxa with closely related extant species. Therefore, the skulls of fossils must be compared to adult skulls of extant taxa in order to directly study the nasal cavity in these fossil taxa.

In this paper, I compared primarily adult specimens of marsupials, but also included data from ontogenetic series and published descriptions of the development of the nasal cavity when available. It is certainly possible that comparative developmental studies may contradict the homology statements I make based on adult specimens. But these comparisons cannot be made until more ontogenetic series are available and published.

The two approaches for studying the nasal cavity use different terminological schemes, producing confusion in the literature (table 3). In this paper, an attempt is made to synthesize this literature and produce a list of synonyms for the terminology for the osteological structures found in adult skulls (appendix 1). For clarity, explicit definitions of the anatomical terms pertaining to the ethmoid and surrounding structures that are used in this paper are presented in appendix 1. In this paper I apply my terminology not only when describing anatomical details, but also when discussing the results of other papers that use different terminological schemes (e.g., Paulli, 1900a, b, c; Moore, 1981) so as to facilitate comparisons.

Phylogenetic Character Matrix

It is the intention of this study to document new characters that might be used in future phylogenetic studies of marsupial relationships. Reductive coding (Wilkinson, 1995) was employed when constructing characters from the morphological observations of the ethmoid to preserve transformational independence between the presence or absence of a particular feature and the variation observable for that feature (Lee and Bryant, 1999). However, multistate characters could easily be constructed from these observations via composite coding if others wish to do so when including these data in their phylogenetic analyses (Wilkinson, 1995).

TABLE 1
Specimen data

Species	Common name	Higher taxon	Specimen No.	Sex	Skull length
<i>Caluromys philander</i>	bare-tailed woolly opossum	Didelphidae	AMNH 95526	♂	58.8 mm
<i>Didelphis virginiana</i>	Virginia opossum	Didelphidae	TMM M-2517	♂	109.6 mm
<i>Monodelphis domestica</i> (adult)	gray short-tailed opossum	Didelphidae	TMM M-7599	♀	40.0 mm
<i>M. domestica</i> (adult)	gray short-tailed opossum	Didelphidae	TMM M-8271	♀	39.9 mm
<i>M. domestica</i> (adult)	gray short-tailed opossum	Didelphidae	TMM M-8273	♂	41.6 mm
<i>M. domestica</i> (adult)	gray short-tailed opossum	Didelphidae	TMM M-9038	?	42.8 mm
<i>M. domestica</i> (27 days old)	gray short-tailed opossum	Didelphidae	TMM M-7595	?	18.5 mm
<i>M. domestica</i> (27 days old)	gray short-tailed opossum	Didelphidae	TMM M-8265	?	14.1 mm
<i>M. domestica</i> (27 days old)	gray short-tailed opossum	Didelphidae	TMM M-8261	?	14.0 mm
<i>M. domestica</i> (48 days old)	gray short-tailed opossum	Didelphidae	TMM M-7536	♀	23.3 mm
<i>M. domestica</i> (48 days old)	gray short-tailed opossum	Didelphidae	TMM M-8269	♀	24.1 mm
<i>M. domestica</i> (56 days old)	gray short-tailed opossum	Didelphidae	TMM M-8266	♀	25.7 mm
<i>M. domestica</i> (57 days old)	gray short-tailed opossum	Didelphidae	TMM M-7539	♀	25.8 mm
<i>M. domestica</i> (~60 days old)	gray short-tailed opossum	Didelphidae	TMM M-9040	?	33.1 mm
<i>M. domestica</i> (~60 days old)	gray short-tailed opossum	Didelphidae	TMM M-9041	?	35.1 mm
<i>M. domestica</i> (~60 days old)	gray short-tailed opossum	Didelphidae	TMM M-9039	?	34.5 mm
<i>M. domestica</i> (75 days old)	gray short-tailed opossum	Didelphidae	TMM M-7542	♂	29.2 mm
<i>M. domestica</i> (76 days old)	gray short-tailed opossum	Didelphidae	TMM M-8267	♂	30.8 mm
<i>M. domestica</i> (90 days old)	gray short-tailed opossum	Didelphidae	TMM M-7545	♀	30.7 mm
<i>M. domestica</i> (90 days old)	gray short-tailed opossum	Didelphidae	TMM M-8268	♂	35.7 mm
<i>Caenolestes fuliginosus</i>	silky shrew opossum	Caenolestidae	KU 124015	♀	28.2 mm
<i>Dasyurus hallucatus</i>	northern quoll	Dasyuridae	TMM M-6921	♀	60.9 mm
<i>Sarcophilus lanarius</i>	Tasmanian devil	Dasyuridae	USNM 307639	♂	139.8 mm
<i>Sminthopsis crassicaudata</i>	fat-tailed dunnart	Dasyuridae	AMNH 196686	♀	22.8 mm
<i>Thylacinus cynocephalus</i>	thylacine	Thylacinidae	AMNH 35244	♂	228.5 mm
<i>Notoryctes typhlops</i>	marsupial mole	Notoryctidae	AMNH 202107	?	26.9 mm
<i>Isodon macrourus</i>	northern brown bandicoot	Peramelidae	TMM M-6922	?	69.0 mm
<i>Echymipera kalubu</i>	common spiny bandicoot	Peramelidae	AMNH 190970	♂	71.5 mm
<i>Dromiciops gliroides</i>	monito del monte	Microbiotheriidae	FMNH 127463	♀	27.7 mm
<i>Macrotis lagotis</i>	greater bilby	Thylacomyidae	AMNH 74486	♀	92.0 mm
<i>Acrobates pygmaeus</i>	feathertail glider	Acrobatidae	AMNH 155057	♀	21.1 mm
<i>Cercartetus caudatus</i>	long-tailed pygmy possum	Burramyidae	AMNH 155090	♂	27.8 mm
<i>Myrmecobius fasciatus</i>	numbat	Myrmecobiidae	AMNH 155328	?	59.0 mm
<i>Tarsipes rostratus</i>	honey possum	Tarsipedidae	AMNH 119717	♂	25.4 mm
<i>Petaurus breviceps</i>	sugar glider	Petauridae	TMM M-8226	♂	35.0 mm
<i>Petauroides volans</i>	greater glider	Pseudocheiridae	AMNH 150055	♀	62.3 mm

TABLE 1
(Continued)

Species	Common name	Higher taxon	Specimen No.	Sex	Skull length
<i>Pseudocheirus occidentalis</i>	common ring-tailed possum	Pseudocheiridae	TMM M-847	?	71.6 mm
<i>Pseudochirops cupreus</i>	coppery ringtail possum	Pseudocheiridae	AMNH 151829	♂	66.6 mm
<i>Phalanger orientalis</i>	gray cuscus	Phalangeridae	AMNH 157211	♀	82.1 mm
<i>Trichosurus vulpecula</i>	silver-gray brush-tailed opossum	Phalangeridae	TMM M-849	?	76.0 mm
<i>Hypsiprymnodon moschatus</i>	musky rat kangaroo	Hypsiprymnodontidae	AMNH 184580	♂	66.0 mm
<i>Potorous tridactylus</i>	long-nosed potoroo	Potoroidae	AMNH 65337	?	92.1 mm
<i>Phascolarctos cinereus</i>	koala	Phascolarctidae	TMM M-2946	?	142.9 mm
<i>Vombatus ursinus</i>	coarse-haired wombat	Vombatidae	TMM M-2953	?	164.9 mm
<i>Dendrolagus lumholtzi</i>	grizzled tree kangaroo	Macropodidae	AMNH 65254	?	109.7 mm
<i>Wallabia bicolor</i>	swamp wallaby	Macropodidae	TMM M-4169	?	139.8 mm
<i>Ornithorhynchus anatinus</i>	duckbill platypus	Ornithorhynchidae	AMNH 200255	?	91.6 mm
<i>Tachyglossus aculeatus</i>	short-snouted echidna	Tachyglossidae	AMNH 154457	♂	99.0 mm
<i>Pteropus lylei</i>	Lyle's flying fox	Pteropodidae	AMNH 237593	♂	63.7 mm
<i>Mus musculus</i>	house mouse	Muridae	TMM M-3196	♀	20.9 mm
<i>Erinaceus</i> sp.	hedgehog	Erinaceidae	TR pers. collect.	?	30.9 mm

However, when dealing with endoturbinals, I follow the current view of turbinal homology, which considers endoturbinals (excluding endoturbinal I) to be serial homologs because they cannot be viewed as developmentally “individualized” (Wagner, 1989; also see discussion below). Consequently, only endoturbinal I is treated as an individualized element for character scoring and the other endoturbinals, which are numbered sequentially, are scored as a collective unit, rather than each being treated in a separate character (e.g., a character for endoturbinal II, another for endoturbinal III, etc.). Similarly, ectoturbinals are viewed as serial homologs and are also scored as a collective unit.

A matrix was scored based on 35 characters from the nasal skeleton (appendix 2) and 29 marsupial taxa and five outgroups (table 1). I then examined the phylogenetic utility of these characters by optimizing the resultant character matrix (appendix 3) on two conflicting topologies for marsupial relationships: one by Meredith et al. (2009) based on analysis of five nuclear genes (fig. 1), and the other by Sánchez-Villagra et al. (2007) based on analysis of morphological data (fig. 2). These two topologies were chosen because they represent recent analyses of phylogenetic relationships within Marsupialia and because they illustrate some of the issues

of contention for interrelationships in this clade as discussed previously. Characters were traced on the tree topologies using parsimony ancestral character state reconstruction in Mesquite (version 2.5, Maddison and Maddison, 2008).

I did not conduct a phylogenetic analysis based solely on the characters described in this paper, because it is not reasonable to base phylogenetic hypotheses on only a single anatomical system. Instead, my characters were optimized on preexisting hypotheses of marsupial intrarelationships to assess their phylogenetic informativeness and to discuss the evolution of the ethmoid within Marsupialia. It is my intention that the new characters described in this paper will be incorporated in future phylogenetic analyses containing matrices that more broadly sample marsupial anatomy.

DESCRIPTION

Osteology of Nasal Cavity as a Whole in Adult Marsupials

The nasal cavity of marsupials is bordered externally by the paired premaxilla, maxilla, nasal, lacrimal, frontal, palatine, and orbitosphenoid bones in the adult skull (fig. 3; Rowe et al., 2005). The premaxilla, maxilla,

TABLE 2
Relevant web addresses

Site Name or Taxon	Web address
UTCT website	<www.ctlab.geo.utexas.edu/overview/index.html>
Digimorph homepage	<www.digimorph.org>
<i>Caenolestes fuliginosus</i>	<www.digimorph.org/specimens/Caenolestes_fuliginosus/>
<i>Cercartetus caudatus</i>	<http://www.digimorph.org/specimens/Cercartetus_caudatus/>
<i>Dasyurus hallucatus</i>	<www.digimorph.org/specimens/Dasyurus_hallucatus/>
<i>Dendrolagus lumholtzi</i>	<www.digimorph.org/specimens/Dendrolagus_lumholtzi/>
<i>Didelphis virginiana</i>	<www.digimorph.org/specimens/Didelphis_virginiana/>
<i>Dromiciops gliroides</i>	<www.digimorph.org/specimens/Dromiciops_gliroides/>
<i>Echymipera kalubu</i>	<www.digimorph.org/specimens/Echymipera_kalubu/>
<i>Isodon macrourus</i>	<www.digimorph.org/specimens/Isodon_macrourus/>
<i>Macrotis lagotis</i>	<www.digimorph.org/specimens/Macrotis_lagotis/>
<i>Monodelphis domestica</i>	<www.digimorph.org/specimens/Monodelphis_domestica/whole/>
<i>Myrmecobius fasciatus</i>	<www.digimorph.org/specimens/Myrmecobius_fasciatus/>
<i>Notoryctes typhlops</i>	<www.digimorph.org/specimens/Notoryctes_typhlops/>
<i>Petauroides volans</i>	<www.digimorph.org/specimens/Petauroides_volans/>
<i>Phalanger orientalis</i>	<www.digimorph.org/specimens/Phalanger_orientalis/>
<i>Phascolarctos cinereus</i>	<www.digimorph.org/specimens/Phascolarctos_cinereus/>
<i>Potorous tridactylus</i>	<www.digimorph.org/specimens/Potorous_tridactylus/>
<i>Pseudocheirus occidentalis</i>	< www.digimorph.org/specimens/Pseudocheirus_occidentalis/>
<i>Pseudochirops cupreus</i>	<www.digimorph.org/specimens/Pseudochirops_cupreus/>
<i>Sarcophilus lanarius</i>	<www.digimorph.org/specimens/Sarcophilus_lanarius/>
<i>Sminthopsis crassicaudata</i>	<www.digimorph.org/specimens/Sminthopsis_crassicaudata/>
<i>Trichosurus vulpecula</i>	<www.digimorph.org/specimens/Trichosurus_vulpecula/>
<i>Vombatus ursinus</i>	<www.digimorph.org/specimens/Vombatus_ursinus/>
<i>Wallabia bicolor</i>	<www.digimorph.org/specimens/Wallabia_bicolor/>
<i>Ornithorhynchus anatinus</i>	<http://www.digimorph.org/specimens/Ornithorhynchus_anatinus/adult/>
<i>Tachyglossus aculeatus</i>	<http://www.digimorph.org/specimens/Tachyglossus_aculeatus/skull/>
<i>Pteropus lylei</i>	<http://www.digimorph.org/specimens/Pteropus_lylei/>
<i>Mus musculus</i>	<http://www.digimorph.org/specimens/Mus_musculus/>

palatine, and orbitosphenoid comprise the floor of the cavity from rostral to caudal. All these elements and the lacrimal contribute to the lateral walls. The nasal cavity is roofed by the nasals and frontals. The rostral end of

the nasal cavity is marked by the confluent external nares, and the caudal wall is formed by the cribriform plate internally.

The nasal cavity communicates with the exterior of the skull via the external nares rostrally and the confluent choanae ventro-caudally. Dorsocaudally, the nasal cavity communicates with the endocranial cavity via the olfactory foramina (for the fibers of cranial nerve I) of the cribriform plate. The ventral floor of the nasal cavity is pierced rostrally by the incisive foramen, which transmits the nasopalatine duct connecting the nasal and oral cavities, a branch of the major palatine artery, and a branch of the caudal nasal nerve (Sánchez-Villagra, 2001; Wible, 2003). The palate of marsupial skulls is also pierced by a large major palatine foramen (maxillary vacuity of Archer, 1976) for the major palatine nerve and artery (Wible, 2003), and sometimes also is

TABLE 3
Terminology for turbinal elements of
Monodelphis domestica

Freyer (1999)	Rowe et al. (2005)
maxilloturbinale	maxilloturbinal
crista semicircularis	nasoturbinal
ethmoturbinale I	endoturbinal I
ethmoturbinale II	endoturbinal II
ethmoturbinale III	endoturbinal IV
ethmoturbinale IV	endoturbinal V
interturbinale	endoturbinal III
frontoturbinale I	ectoturbinal I
frontoturbinale II	ectoturbinal 2

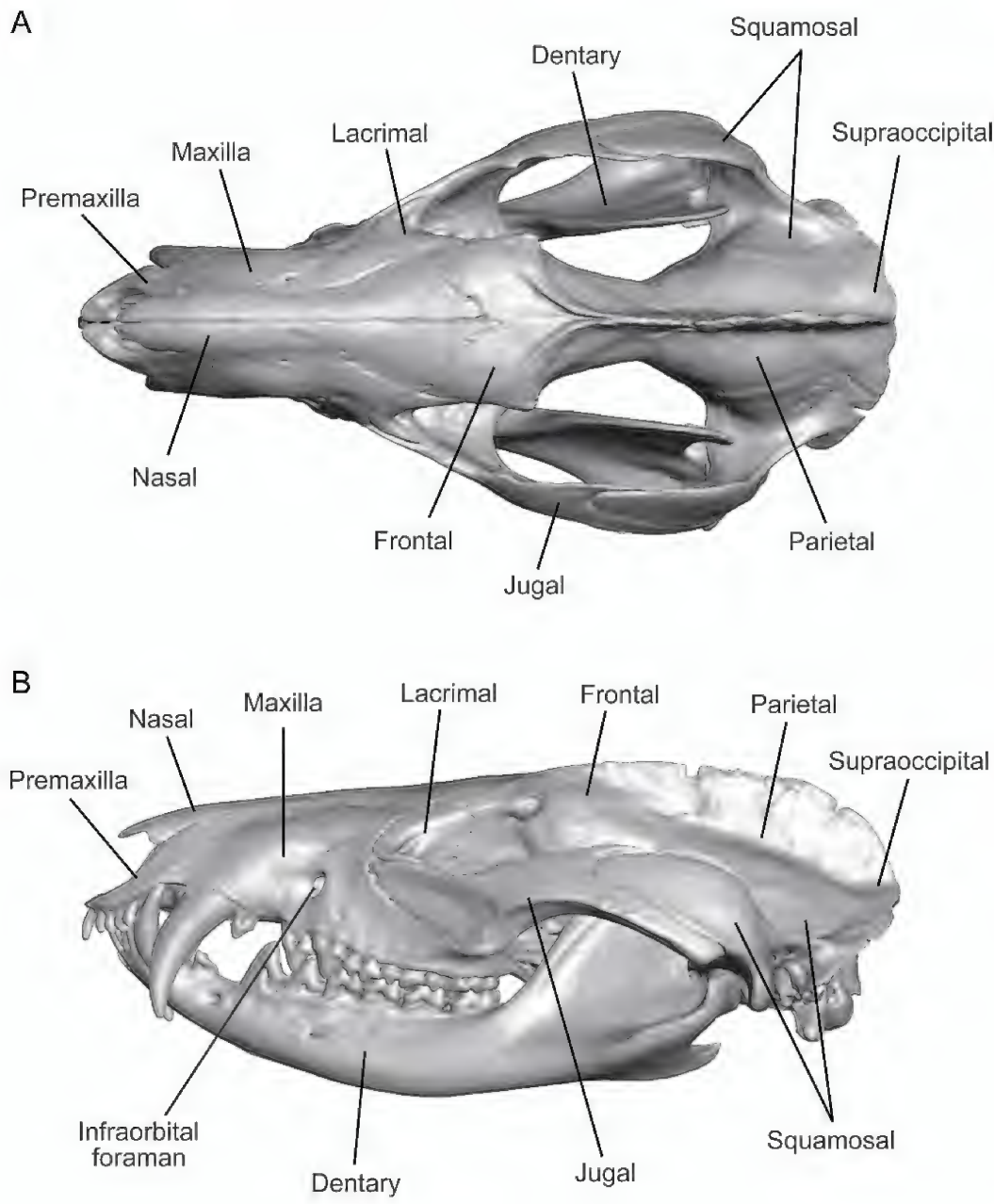


Fig. 3. Skull of *Didelphis virginiana* (TMM M-2517) shown in (A) dorsal, and (B) left lateral views. Scale bar equals 1 cm.

pierced by a separate palatine vacuity (Archer, 1976). The dorsolateral wall of the nasal cavity communicates with the exterior via one or more foramen of the lacrimal bone, through which

passes the nasolacrimal duct and accompanying vein (Archer, 1976; Wible, 2003).
The right and left halves of the nasal cavity are divided internally by the nasal septum

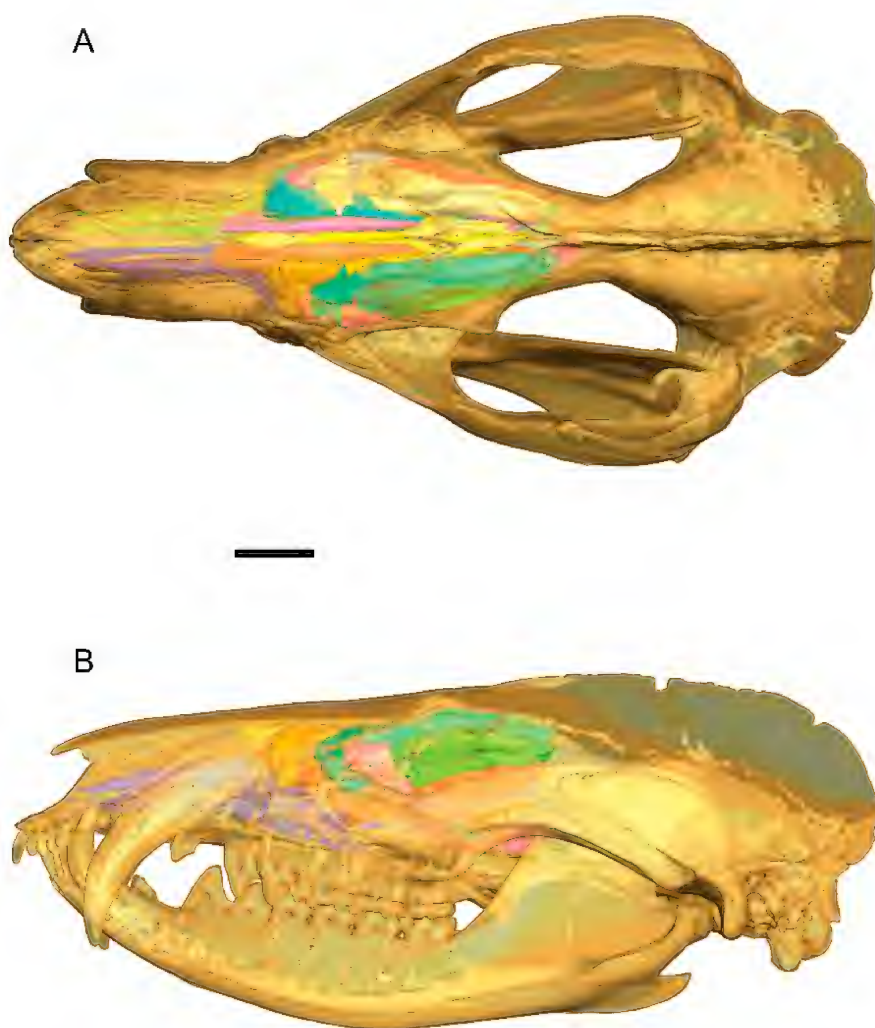


Fig. 4. Digital rendering of the ethmoid bones (shown in color) inside the semitransparent skull of *Didelphis virginiana* (TMM M-2517) shown in (A) dorsal, and (B) left lateral views. Scale bar equals 1 cm.

(figs. 4 and 5) whose rostral one-third is cartilaginous and the remaining caudal portion is ossified in adult marsupials. The ossified nasal septum in marsupials results from a rostral advancement of endochondral ossification from a center ventral to the developing olfactory bulbs of the brain (Broom, 1926; Clark and Smith, 1993; Rowe et al., 2005). Both the cartilaginous and ossified portions of the nasal septum of adult marsupials articulate ventrally with a V-shaped median groove formed by the dorsal surface of the vomer.

An ethmoid bone is present for each half of the nasal cavity in adult marsupials

(fig. 5). This is contra the condition in humans in which the right and left elements fuse with the ossified nasal septum to form a single, midline element in adults (Gray, 1977). Each ethmoid comprises several complexly scrolled elements known as turbinals, including the maxilloturbinal, nasoturbinal, ectoturbinals, and endoturbinals (figs. 4 and 5; Rowe et al., 2005). The maxilloturbinal (inferior nasal concha in humans), which arises from its own ossification center (Gray, 1977) is considered here as part of the compound ethmoid bone because it develops in the epithelium of the nasal cavity as do the other turbinals (*sensu* Rowe et al., 2005).

This is contra the usage in human anatomical terminology.

The endoturbinals coalesce caudally with the paraseptal shelf of the vomer to form the posterior transverse lamina, which forms the roof of the nasopharyngeal meatus (fig. 5; Rowe et al., 2005). Sometimes the ventral-most ectoturbinal will contact the rostral portion of the posterior transverse lamina. Caudal to the posterior transverse lamina, the nasoturbinal, ectoturbinals, and endoturbinals coalesce to form the cribriform plate (fig. 5). The cribriform plate marks the caudal border of the nasal cavity and the rostral border of the endocranial cavity for the brain and associated soft tissue structures. The portion of the ossified nasal septum that traverses the cribriform plate and enters the endocranial cavity is called the crista galli.

The turbinal elements define a series of complex passages for air flow through the nasal cavity. These bony elements and the internal walls of the nasal cavity are covered by either respiratory or olfactory epithelium, thus indicating the function of the individual passages.

The sphenethmoid recess is the space divided by the nasal septum and occupied by all the turbinal elements; the surfaces of this space are lined by either respiratory or olfactory epithelium (fig. 6; Rowe et al., 2005). This recess comprises all the space within the nasal cavity except for the nasopharyngeal meatus (fig. 6). The sphenethmoid recess is floored caudally by the posterior transverse lamina and is roofed by the cribriform plate (Rowe et al., 2005). The caudalmost extent of the sphenethmoid recess is named the sphenoidal recess (Miller et al., 1964).

The paired nasopharyngeal meatus is the portion of the nasal cavity that is roofed by the posterior transverse lamina and leads to the choanae (fig. 6). This space is lined by respiratory epithelium in *Monodelphis domestica* and is devoid of turbinal elements (Rowe et al., 2005).

Besides the respiratory and olfactory epithelia, additional soft tissue structures, such as the lateral nasal gland and vomeronasal organ, are also located in the nasal cavity. The lateral nasal gland produces

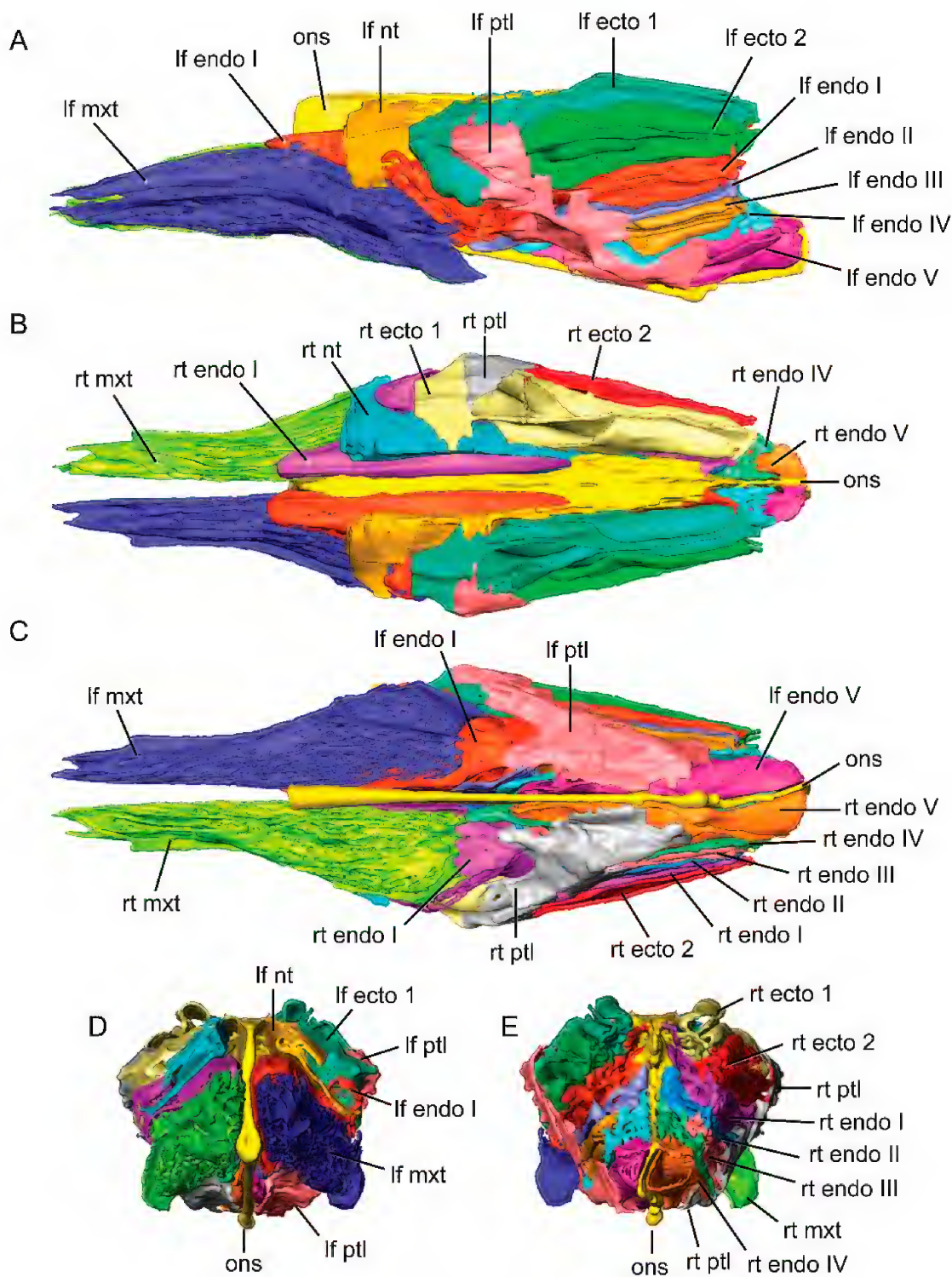
mucus for the epithelia and is located in the lateral recess (Miller et al., 1964; Rowe et al., 2005). The lateral nasal gland is variably present in adult marsupials, being well developed in *Isodon macrourus* and *Tarsipes rostratus*, but absent in *Phascogale cinereus* (Kratzing, 1978, 1982, 1984).

The vomeronasal organ (VNO) functions in the detection of pheromones, playing a role in intraspecific communication (Døving and Trotter, 1998; Keverne, 1999). The VNO and surrounding structures comprise the vomeronasal complex (Sánchez-Villagra, 2001). The vomeronasal complex of marsupials includes a vomeronasal organ and accompanying nasopalatine duct, but lacks a nasopalatine duct cartilage and has no or only incipient palatine cartilage (Sánchez-Villagra, 2001). In postnatal development, the paraseptal cartilage forms the capsule for housing the VNO, located caudal to the anterior transverse lamina and lateral to the rostral nasal septum (Sánchez-Villagra, 2001). In the adult marsupial skull, the VNO lies along the paraseptal shelf of the vomer at the base of the ossified nasal septum (Rowe et al., 2005).

Cartilaginous Elements of Adult Marsupials

Some cartilaginous elements of the nasal capsule related to the developing nasal capsule are retained in adult specimens of mammals (Voit, 1909; Freyer, 1999; Maier, 2000). These elements do not ossify and are not often preserved in skeletonized adult specimens, but are still worth mentioning here. These elements include the marginoturbinal, atrioturbinal, and anterior transverse lamina.

The marginoturbinal is an enrolling of the ventral surface of the cartilaginous nasal cavity roof (Voit, 1909; Freyer, 1999; Maier, 2000). Rostrally, the marginoturbinal begins at the lateral margin of the external naris and caudally, it continues as the atrioturbinal and connects with the maxilloturbinal (Maier, 2000). Therefore, the atrioturbinal is a cartilaginous caudal extension of the marginoturbinal (Maier, 2000). The anterior transverse lamina comprises a cartilaginous pillar that supports the nasal cupula and the atrioturbinal (Maier, 2000).



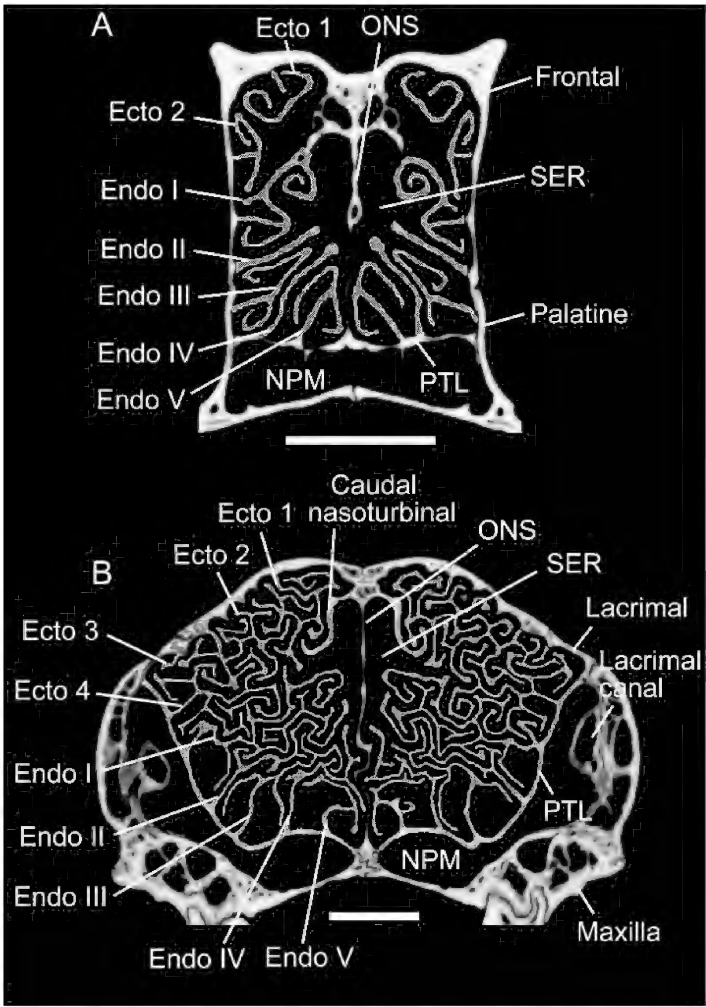


Fig. 6. Coronal CT images showing the packing of endo- and ectoturbinals (char. 14). (A) turbinals are relatively loosely packed (char. 14.0), *Caluromys philander*, C330 (AMNH 95526); (B) turbinals are complexly branching or convoluted elements that are densely packed creating a tight mazelike pattern, especially around the ossified nasal septum (char. 14.1), *Potorous tridactylus*, C440 (AMNH 65337). Both scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; NPM, nasopharyngeal meatus; ONS, ossified nasal septum; PTL, posterior transverse lamina; SER, sphenethmoid recess.

←

Fig. 5. Digital rendering of both ethmoids and the ossified nasal septum of *Didelphis virginiana* (TMM M-2517) shown in (A) left lateral, (B) dorsal, (C) ventral, (D) rostral, and (E) caudal (encranial) views. For A–C, rostral is to the left. For A, D, E, dorsal is towards the top of the page. Scale bar equals 1 cm; all images to the same scale. Abbreviations: lf, left (preceding structure abbreviation); rt, right (preceding structure abbreviation); ecto, ectoturbinal (followed by an Arabic numeral); endo, endoturbinal (followed by a Roman numeral); mxt, maxilloturbinal; nt, nasoturbinal; ons, ossified nasal septum; ptl, posterior transverse lamina.

Maxilloturbinal

The maxilloturbinal attaches to the internal surface of the maxilla and is the most extensive turbinal in the skull. At its rostral extremity, the maxilloturbinal is typically the only turbinal element occupying the nasal cavity. However, in some marsupials (see below) and at least some placentals (e.g., many armadillos, Gaudin and Wible, 2006; *Solenodon*, Wible, 2008), the nasoturbinal is the rostralmost turbinal element.

Caudally, the maxilloturbinal lies ventral to the anteriormost projection of endoturbinal I and medioventral to the nasoturbinal. The caudal extremity of the maxilloturbinal extends nearly to the rostral edge of the posterior transverse lamina. The maxilloturbinal does not typically contact any of the other turbinal elements in marsupials. The surface of the maxilloturbinal is covered by respiratory epithelium in *Monodelphis domestica* (Rowe et al., 2005).

In most marsupials, the rostral portion of the maxilloturbinal is arborlike with many branches (figs. 5 and 7). This is particularly apparent if the maxilloturbinal is examined in the same coronal plane as the rostral portion of the roots of the upper canines. The rostralmost attachment point of the maxilloturbinal is usually on the lateral wall of the nasal cavity rostral or even with the rostral portion of the roots of the upper canines.

The caudalmost attachment point of the maxilloturbinal of most marsupials is on the floor of the nasal cavity. At this point, the maxilloturbinal is simple in morphology with only a few branches or scrolls.

Nasoturbinal

The nasoturbinal is located dorsolateral to the maxilloturbinal (fig. 5) and is typically the second turbinal visible when navigating through the skull from rostral to caudal. The nasoturbinal is a complex, bony element in the adult mammalian skull that is recognized here as a compound structure. The rostral portion of the nasoturbinal (henceforth “rostral nasoturbinal”) corresponds with the ossification of a compound structure developing from a medial contribution from the ventral folding of the tectum and a lateral contribution formed from

a portion of the pars anterior of the paries nasi (figs. 8 and 9; Smith and Rossie, 2006). The caudal nasoturbinal of this paper corresponds to the ossification of the crista semicircularis. The crista semicircularis is formed from the overlap between the pars anterior and pars intermedia of the paries nasi in the chondrocranium (fig. 8; Rossie, 2006; Smith and Rossie, 2006). The projection of the caudal portion of the pars anterior into the nasal capsule is the crista semicircularis (fig. 8).

Many, but not all, marsupials have a rostral nasoturbinal present as an ossified element in the adult skull (fig. 9). The rostral nasoturbinal is a small, robust bony process with a ventromedial inflection in slightly more than half of those taxa that have the element as adults (fig. 10). In the remaining taxa the rostral nasoturbinal has a slender ventromedially directed morphology (fig. 10).

All the marsupial skulls I examined have an ossified caudal nasoturbinal, and in those taxa with a rostral nasoturbinal, both the rostral and caudal nasoturbinal elements are fused as a continuous bony structure (e.g., *Dasyurus hallucatus*). The rostral portion of the caudal nasoturbinal is often seen in the same coronal section as the maxilloturbinal and the rostral portion of endoturbinal I (e.g., C190–200 in *Dasyurus*). The caudal nasoturbinal forms the medial border of the lateral recess (figs. 8 and 11), a space that sometimes is divided by the root of endoturbinal I into a dorsal space (frontal recess) containing the ectoturbinals and a ventral space (maxillary recess). The medial surface of the caudal nasoturbinal that faces the ossified nasal septum is covered by olfactory epithelium, whereas the lateral surface facing into the lateral recess is covered mainly by respiratory epithelium in *Monodelphis domestica* (Rowe et al., 2005).

The caudal nasoturbinal of marsupials is usually unbranched and typically lacks pneumatic vacuities (fig. 12). There are two attachment points of the rostral part of the caudal nasoturbinal to the nasal cavity. The rostro-dorsal attachment is typically on the nasal cavity roof, and the rostroventral attachment is located on the lateral wall of the nasal cavity.

The morphology of the rostral part of the caudal nasoturbinal is typically of two types. In some marsupials (e.g., *Monodelphis*

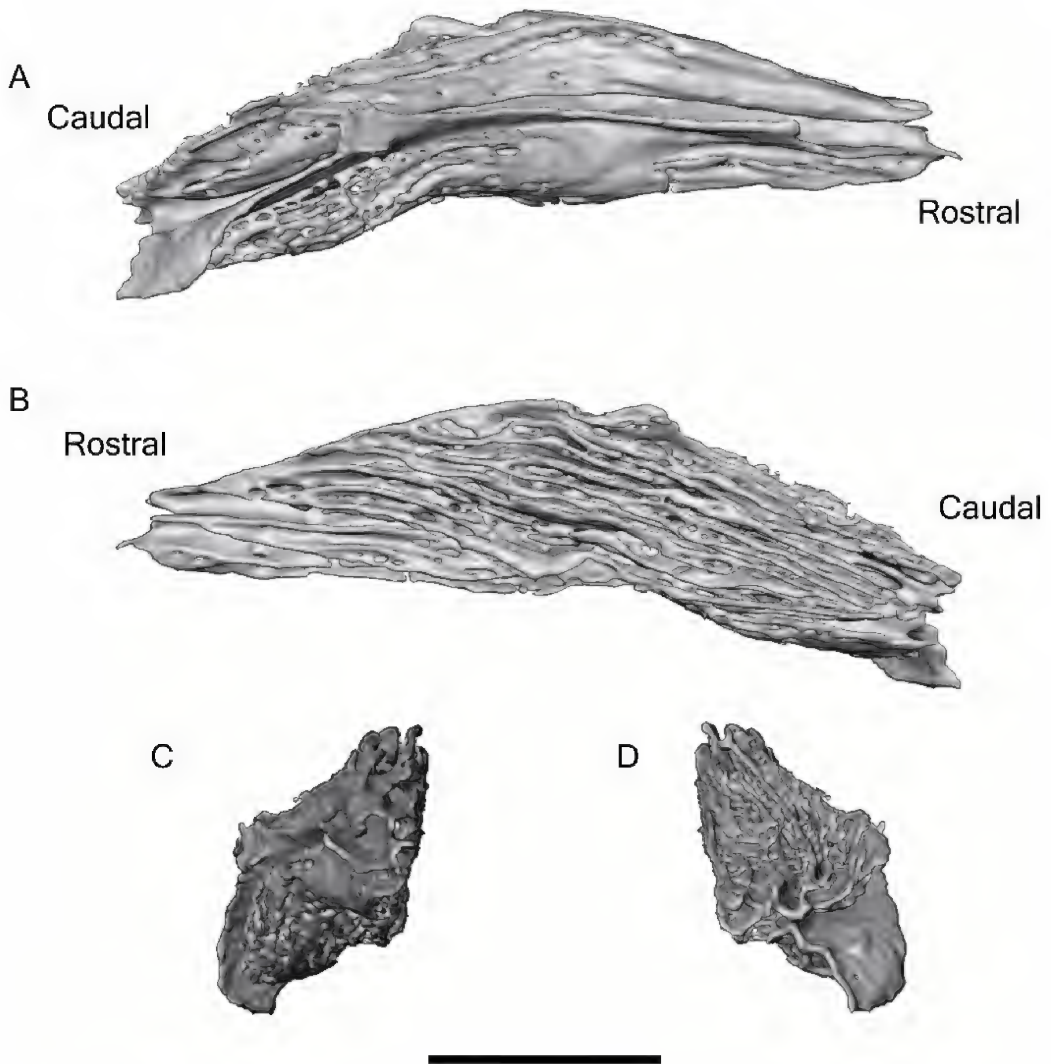


Fig. 7. Digital rendering of the isolated right maxilloturbinal from *Didelphis virginiana* (TMM M-2517) shown in (A) lateral, (B) medial, (C) rostral, and (D) caudal views. Labels indicate caudal and rostral ends of the maxilloturbinal for the lateral and medial views. Scale bar equals 1 cm.

domestica, Rowe et al., 2005), the rostral portion is straight and oriented parallel to the portion of the maxilla forming the nasal cavity lateral wall and at an oblique angle to the ossified nasal septum (fig. 11). However, in most marsupials there is a distinctive kink between the rostradorsal and rostroventral portions of the caudal nasoturbinal (fig. 11). The rostradorsal and rostroventral portions of the lateral face of the caudal nasoturbinal are typically kinked at an acute or nearly a right angle to each other.

Caudally, the caudal nasoturbinal divides around endoturbinal I, as was described for *Monodelphis domestica* (Rowe et al., 2005), in nearly all of the marsupials examined here. The caudodorsal portion of the caudal nasoturbinal usually remains unfolded (fig. 13). The uncinate process, which is the caudodorsal attachment of the caudal nasoturbinal that remains caudal to the division of the nasoturbinal around endoturbinal I, is absent as an ossified structure in the majority of marsupials (fig. 14).

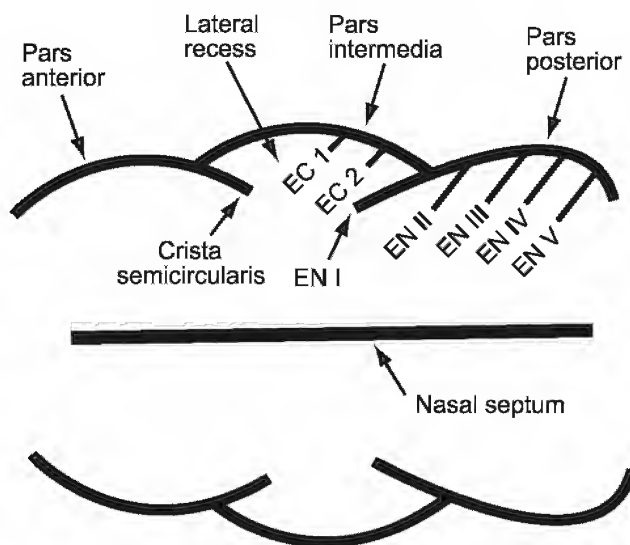


Fig. 8. Schematic diagram showing a dorsal view of the paries nasi of the chondrocranium of a marsupial. Rostral is to the left. Figure modeled after Smith and Rossie (2006: fig. 8.4). Abbreviations: EC, ectoturbinal; EN, endoturbinal.

The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the lacrimal canal or the lateral wall of the nasal cavity (fig. 15). The caudalmost extent of the ventral attachment of the nasoturbinal is near the caudal terminus of the maxilloturbinal, whereas the dorsocaudal portion of the caudal nasoturbinal contributes to the cribriform plate (fig. 16).

Endoturbinals

The endoturbinals are the turbinal elements lying beneath the ectoturbinals (Allen, 1882; fig. 17; appendix 1). Endoturbinals span the entire height of the sphenethmoidal recess and their distal ends coalesce to form the ethmoid plate of the posterior transverse lamina and their bases come together to form the roof of the sphenethmoid recess around the olfactory bulbs (Rowe et al., 2005).

Endoturbinals are named with Roman numerals from anterodorsal to posteroventral in the nasal cavity based on the position of the respective bases of these elements, such that the base of endoturbinal I is dorsal to that of endoturbinal II (fig. 17). Some authors refer to the nasoturbinal as endoturbinal I (Paulli, 1900a, 1900b, 1900c; Moore, 1981; fig. 17), but this convention is

not followed here (see appendix 1 for justification). Instead the first endoturbinal has its base caudal and ventral to the dorsal attachment of the nasoturbinal, following the convention of other authors (Allen, 1882; Rowe et al., 2005; Giannini et al., in review; fig. 17).

This numbering system reflects the current view of turbinal homology, which is that the endoturbinals below endoturbinal I (e.g., endoturbinal II, III, IV, etc.) are serially homologous (Rowe et al., 2005; Rossie, 2006, 2008). Support for this view is summarized by Rossie (2006), who points out that these endoturbinals chondrify as rudiments of successive endoturbinals, are identified solely on their relative position, and the number of these elements is variable within species. Endoturbinals cannot be viewed as developmentally “individualized” (Wagner, 1989), and consequently it is not possible to determine which elements are homologous across taxa if they have different numbers of endoturbinals.

The typical marsupial condition is the presence of five endoturbinals (fig. 17), but this number varies between three and seven across Marsupialia (table 4; fig. 18). Endoturbinals are covered by olfactory epithelium in *Monodelphis domestica* with the exception

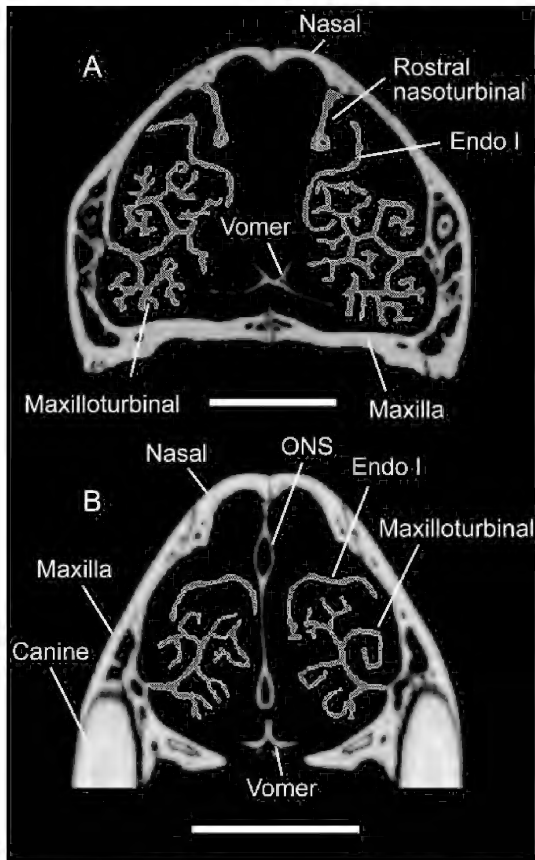


Fig. 9. Coronal CT images showing the presence or absence of an ossified rostral nasoturbinal (char. 5). (A) rostral nasoturbinal is present (char. 5.0), *Dasyurus hallucatus*, C160 (TMM M-6921); (B) rostral nasoturbinal is absent (char. 5.1), *Caluromys philander*, C109 (AMNH 95526). Both scale bars equal 5 mm. Abbreviations: Endo, endoturbinal; ONS, ossified nasal septum.

that the rostroventral surface of endoturbinal I is covered by respiratory epithelium (Rowe et al., 2005).

Despite the fact that the endoturbinas (excluding endoturbinal I) are considered to be serial homologs, there are recognizable morphological differences in adult forms of these elements. The endoturbinas are described below as they typically appear in marsupials with five elements (e.g., *Didelphis virginiana*, figs. 5 and 17).

ENDOTURBINAL I: The first endoturbinal is the largest and most complex of the endoturbinas; it also projects the most rostrally. In

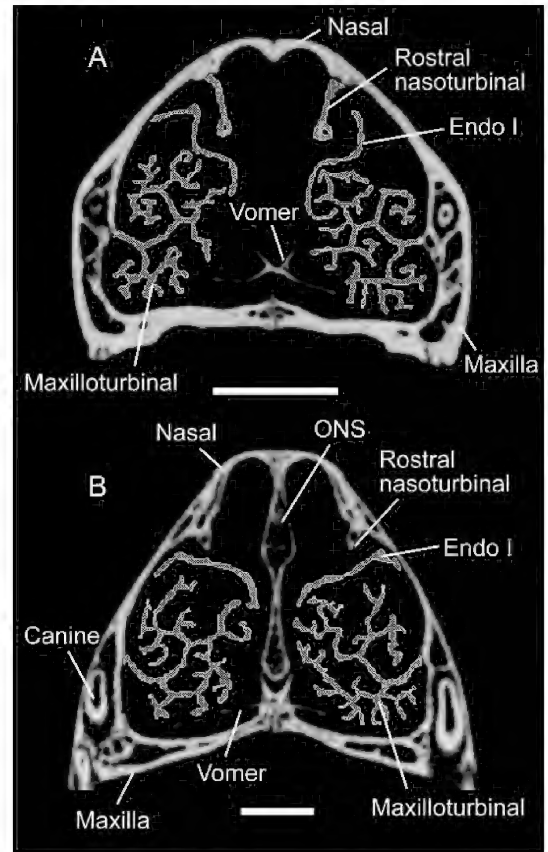


Fig. 10. Coronal CT images showing the morphology of the ossified rostral nasoturbinal (char. 6). (A) rostral nasoturbinal is well developed as a slender ventromedial directed process (char. 6.0), *Dasyurus hallucatus*, C160 (TMM M-6921), scale bar equals 5 mm; (B) rostral nasoturbinal is a small, robust bony process with a ventromedial inflection (char. 6.1), *Dromiciops gliroides*, C136 (FMNH 127463), scale bar equals 1 mm. Abbreviations: Endo, endoturbinal; ONS, ossified nasal septum.

some marsupial taxa endoturbinal I projects more rostrally than the nasoturbinal (fig. 5). The rostralmost extension of endoturbinal I arches above the maxilloturbinal, forming a ventrally concave roof over the latter element, effectively providing a partition between the olfactory (above) and respiratory (below) portions of the nasal cavity (Rowe et al., 2005; figs. 5 and 19). The rostral portion of endoturbinal I of marsupials usually contains pneumatic vacuities (fig. 19).

Typically, the caudal portion of endoturbinal I of marsupials has one turbinal fold and

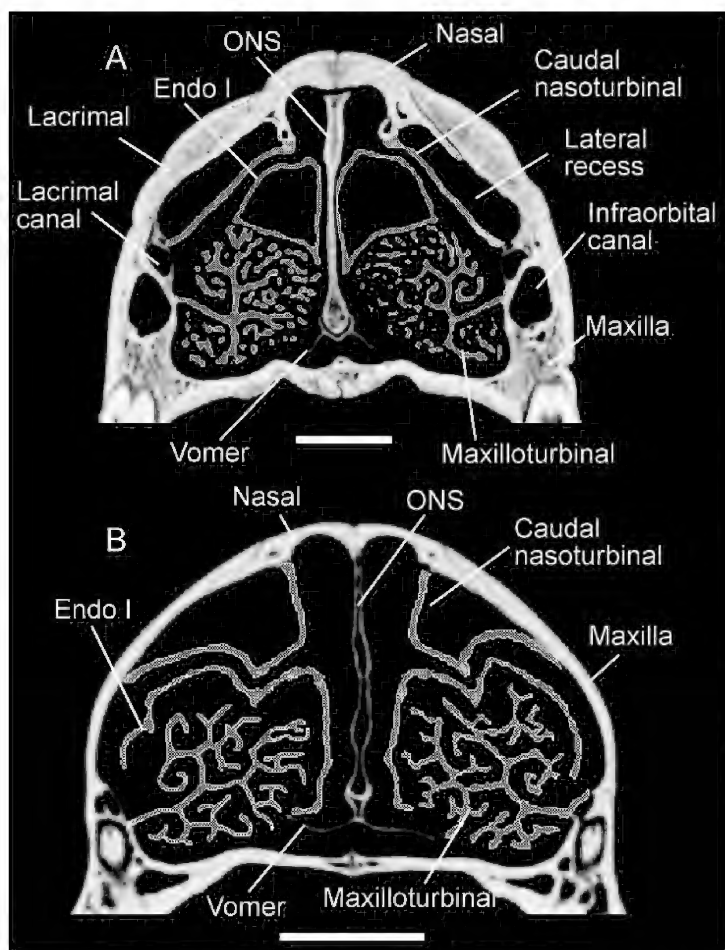


Fig. 11. Coronal CT images showing the morphology of the rostral portion of the caudal nasoturbinal (char. 9). (A) rostradorsal and rostroventral portions are straight (without a kink; char. 9.0), *Didelphis virginiana*, C270 (TMM M-2517); (B) distinctive kink between rostradorsal and rostroventral portions of caudal nasoturbinal (char. 9.1), *Dasyurus hallucatus*, C208 (TMM M-6921). Both scale bars equal 5 mm. Abbreviations: Endo, endoturbinal; ONS, ossified nasal septum.

three turbinal lobes that branch from a single lamella attached to the nasal cavity wall (fig. 20). This caudal morphology of endoturbinal I was examined at the level at which all endoturbinals and ectoturbinals are visible in the same coronal plane or slice (fig. 17). This slice is through the orbits and usually contains the following surrounding anatomical structures: zygomatic arch or rostral root of the arch, frontal bone roofing the nasal cavity, and a section through the penultimate or ultimate pair of upper and lower molars.

ENDOTURBINAL II: The second endoturbinal of marsupials is typically a simple element that is unbranched at its medial

terminus (Rowe et al., 2005; fig. 17). Endoturbinal II is not as rostrocaudally or mesolaterally extensive as endoturbinal I, yet the second endoturbinal contributes to the cribriform plate as do all of the endoturbinals. Rostrally, the lamella of endoturbinal II is attached to the posterior transverse lamina, but caudally the lamella is attached to the lateral wall of the nasal cavity.

ENDOTURBINAL III: The third endoturbinal is typically the smallest of the endoturbinals (fig. 5). Endoturbinal III does not extend as far medially into the nasal cavity lumen as do the other endoturbinals (fig. 17); therefore, the septoturbinal space between

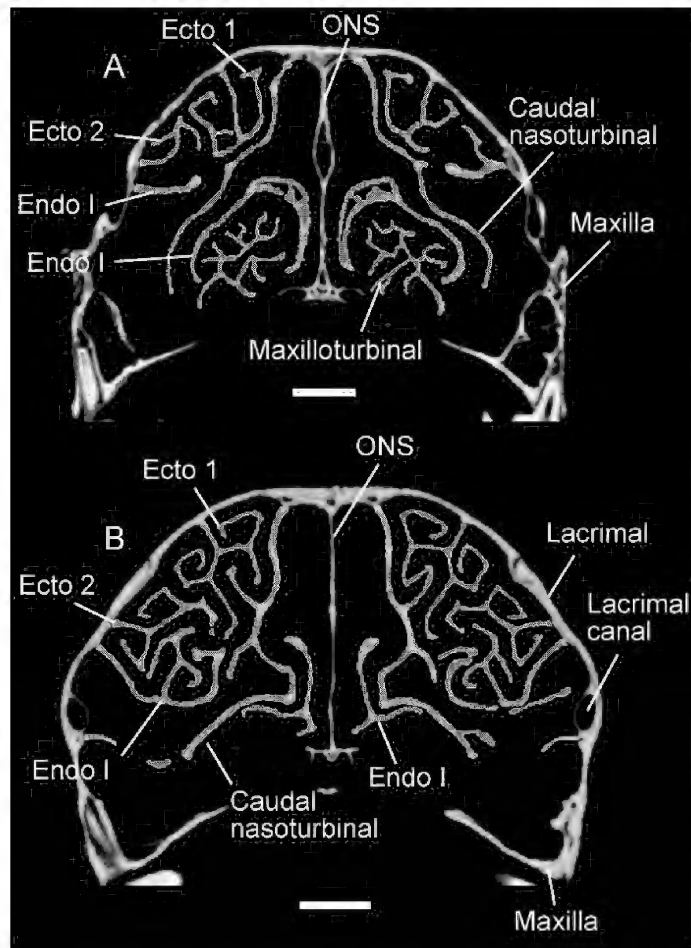


Fig. 12. Coronal CT images showing the morphology of the caudal nasoturbinal (char. 7). (A) caudal nasoturbinal is unbranched (char. 7.0), *Dromiciops gliroides*, C230 (FMNH 127463); (B) caudal nasoturbinal has at least one branch (char. 7.1), *Caenolestes fuliginosus*, C389 (KU 124015). Both scale bars equal 1 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum.

this element and the ossified nasal septum is greater than that of any of the other endoturbinals (Rowe et al., 2005). Endoturbinal III has a bifurcate morphology with each branch ending in a scroll, although the rostral portion of this element may have secondary branching along one of these primary branches (fig. 17). Rostrally, the lamella of endoturbinal III is attached to the posterior transverse lamina, but caudally the lamella is attached to the lateral wall of the nasal cavity.

ENDOTURBINAL IV: The fourth endoturbinal, similar to endoturbinal II, is a simple element with few if any branches (fig. 17).

The rostral portion of endoturbinal IV is typically unbranched but may contain a terminal bifurcation, whereas the caudal portion of this endoturbinal near its contribution to the cribriform plate is almost always unilaminar in marsupials. Similar to endoturbinals II and III, the fourth endoturbinal is attached to the posterior transverse lamina rostrally, and caudally its lamella is attached to the lateral wall of the nasal cavity.

ENDOTURBINAL V: The fifth endoturbinal is typically the caudalmost turbinal of any sort (fig. 5), being sequestered into the sphenoidal recess, the caudal extension of

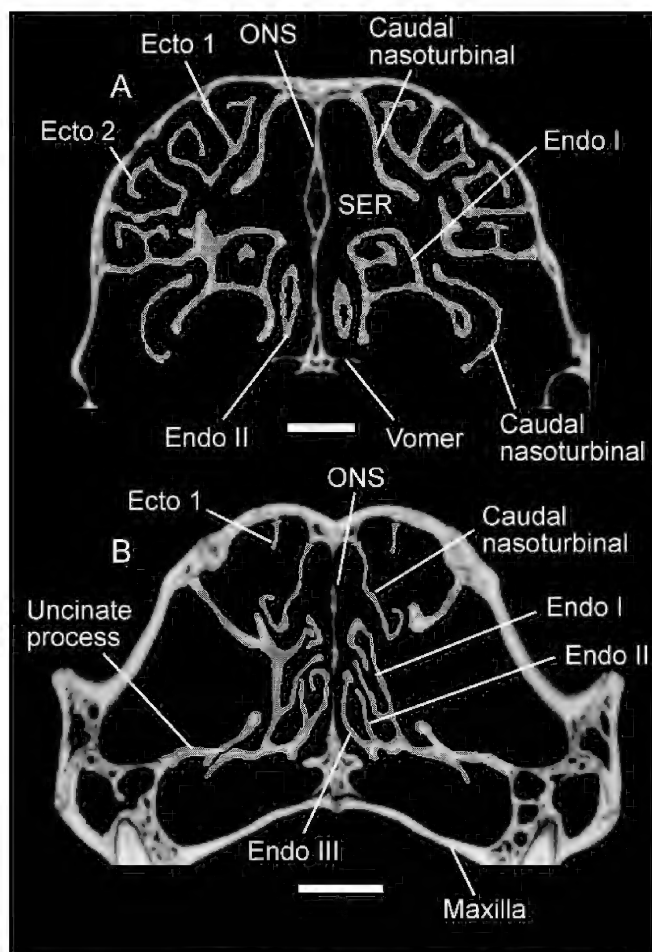


Fig. 13. Coronal CT images showing the morphology of the caudodorsal portion of caudal nasoturbinal (caudal to nasoturbinal division around endoturbinal I; char. 10). (A) caudodorsal portion is unfolded (ch. 10.0), *Dromiciops gliroides*, C245 (FMNH 127463), scale bar equals 1 mm; (B) caudodorsal portion curls (char. 10.1), *Phalanger orientalis*, C250 (AMNH 157211), scale bar equals 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; SER, sphenethmoid recess.

the nasal cavity into the orbitosphenoid (Rowe et al., 2005). The caudal portion of endoturbinal V, which is sequestered into the sphenoidal recess, is typically bilaminar with each branch ending in a scroll. The rostral portion of endoturbinal V is attached to the posterior transverse lamina similar to endoturbinals II–IV. However, caudally the lamella of endoturbinal V may be attached to the lateral wall or floor of the nasal cavity at the rostralmost point of contribution of the turbinal to the cribriform plate. At this point, the turbinal folds of endoturbinal V are typically symmetrical in size.

Ectoturbinals

The ectoturbinals are sequestered in the frontal recess between the nasoturbinal and endoturbinal I (appendix 1). The morphology of marsupial ectoturbinals is generally of a bifurcating element with each branch terminating in a scroll (figs. 5 and 17), although not all ectoturbinals bifurcate. Ectoturbinals are covered with olfactory epithelium in *Monodelphis domestica* (Rowe et al., 2005).

Marsupials typically have two ectoturbinals, but the number varies between one and

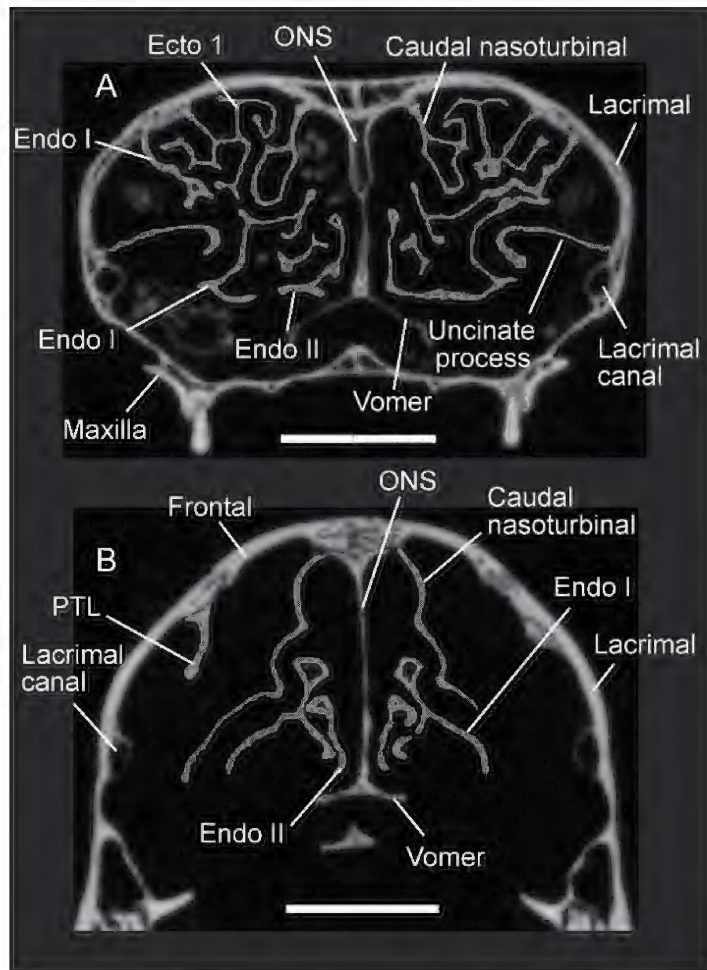


Fig. 14. Coronal CT images showing the presence or absence of an uncinat process of the nasoturbinal (char. 11). (A) uncinat process present (char. 11.0), *Myrmecobius fasciatus*, C270 (AMNH 155328); (B) uncinat process absent (char. 11.1), *Echymipera kalubu*, C435 (AMNH 190970). Both scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; PTL, posterior transverse lamina.

four (table 4; fig. 21). The currently accepted convention is to number ectoturbinals from dorsal to ventral with Arabic numerals, such that ectoturbinal 1 is dorsal to ectoturbinal 2. This numbering scheme reflects the current view that ectoturbinals, like endoturbinals, are serially homologous. Furthermore, the similarity of form of most ectoturbinals prevents making homology statements about the elements based on adult morphology. That is, it is not clear whether ectoturbinal 2 of a marsupial with three ectoturbinals is homologous to ectoturbinal 2 of a marsupial

with only two ectoturbinals. Similarly, if a marsupial only has one ectoturbinal, it is unclear whether it corresponds to ectoturbinal 1 or 2 of a marsupial with two ectoturbinals.

The lamella of the ventralmost ectoturbinal is typically closely associated with the lamella of endoturbinal I rostrally, and often it is attached to the posterior transverse lamina. Caudally, the lamellae of the ectoturbinals are attached to the lateral wall or roof of the nasal cavity. Ectoturbinals typically contribute to the cribriform plate.

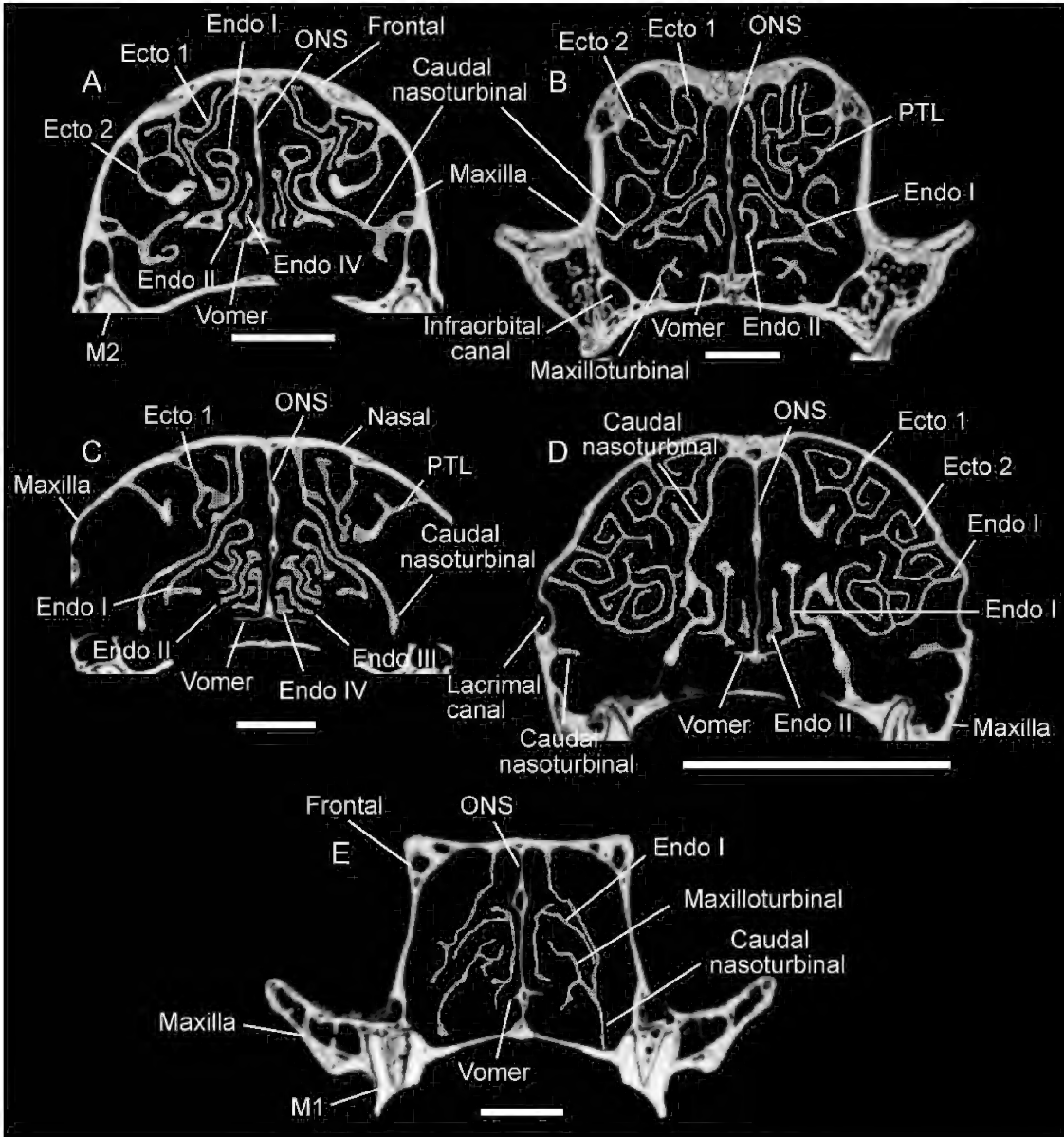


Fig. 15. Coronal CT images showing the caudalmost point of ventral attachment of caudal nasoturbinal (char. 12). (A) nasoturbinal attaches to medial wall of lacrimal canal (char. 12.0), *Isoodon macrourus*, C374 (TMM M-6922); (B) nasoturbinal attaches to lateral wall of nasal cavity (char. 12.1), *Trichosurus vulpecula*, C212 (TMM M-849); (C) nasoturbinal attaches to medial wall of infraorbital canal (char. 12.2), *Dasyurus hallucatus*, C286 (TMM M-6921); (D) nasoturbinal attaches to floor of nasal cavity (char. 12.3), *Caenolestes fuliginosus*, C408 (KU 124015); (E) nasoturbinal attaches to the maxilloturbinal (char. 12.4), *Petauroides volans*, C450 (AMNH 150055). All scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; PTL, posterior transverse lamina.

Posterior Transverse Lamina

The posterior transverse lamina is a compound structure that is formed rostrally by

the caudal portions of the endoturbinals and caudally by the vomer (Rowe et al., 2005; fig. 5). The portion of the posterior transverse lamina constructed from the endoturbinals is

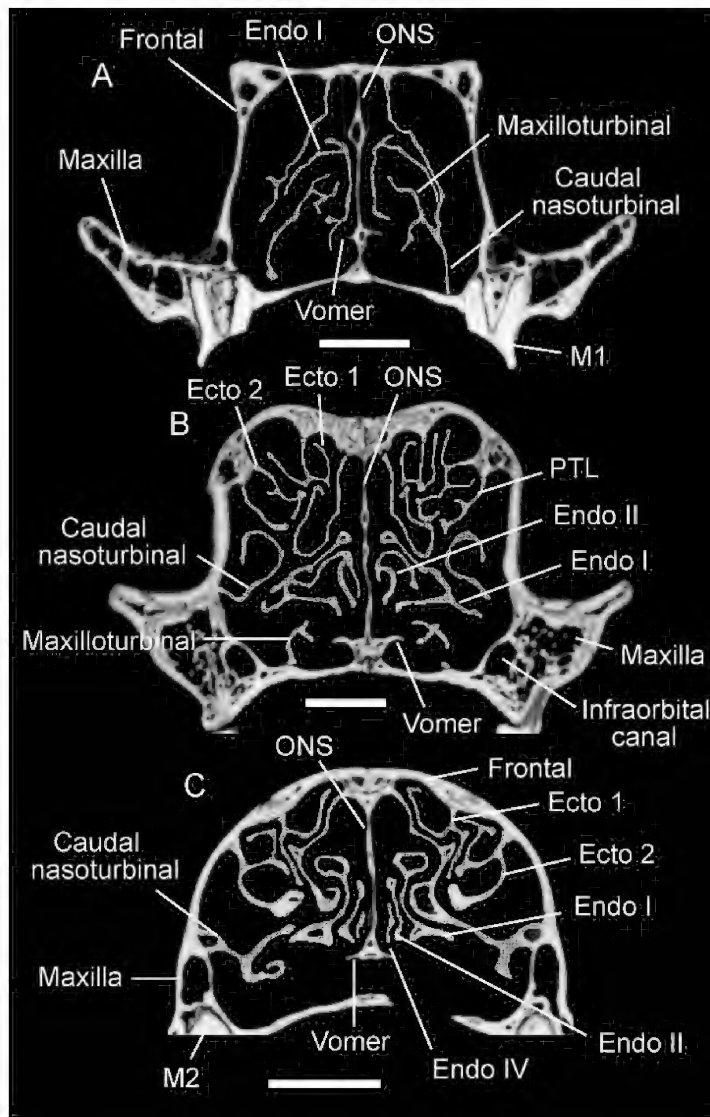


Fig. 16. Coronal CT images showing the caudalmost extent of ventral attachment of nasoturbinal (char. 13). (A) attachment is rostral to caudal terminus of maxilloturbinal (char. 13.0), *Petauroides volans*, C450 (AMNH 150055); (B) attachment is at coronal level of caudal terminus of maxilloturbinal (char. 13.1), *Trichosurus vulpecula*, C212 (TMM M-849); (C) attachment is caudal to caudal terminus of maxilloturbinal (char. 13.2), *Isodon macrourus*, C374 (TMM M-6922). All scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; PTL, posterior transverse lamina.

called the *ethmoid plate* (Rowe et al., 2005), and the portion formed by the paraseptal shelf of the vomer is called the *turbino-vomerine lamina* (Allen, 1882). Although the ectoturbinals do not contribute to the posterior transverse lamina, the ventralmost ectoturbinal may contact the rostral portion of the lamina (fig. 22).

The rostralmost extension of the posterior transverse lamina is just caudal to posterior-most coronal section through which the medial wall of the lateral recess is complete. Caudally, the posterior transverse lamina contributes to the roof of the nasopharyngeal meatus, but the lamina rarely contributes to the cribriform plate. The posterior transverse

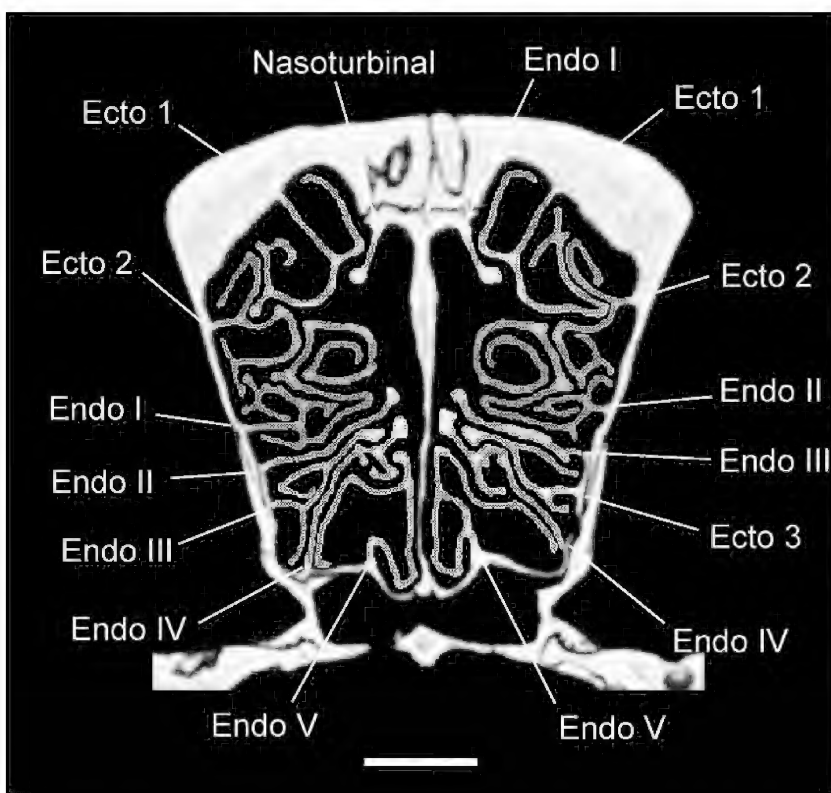


Fig. 17. Coronal CT slice through the nasal cavity of *Didelphis virginiana*, C432 (TMM M-2517) showing two different terminology schemes for naming ectoturbinals and endoturbinals. Left side of figure is labeled with terminology following Allen (1882), which is used in this paper. Right side of figure is labeled using terminology of Paulli (1900a). Scale bar equals 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal.

lamina is typically widest rostrally stretching from the nasal cavity lateral wall to the ossified nasal septum, and caudally the lamina narrows with the nasal cavity. The rostral portion of the posterior transverse lamina is typically oriented parallel or sub-parallel to the palate in marsupials such that it is perpendicular to the ossified nasal septum. As the posterior transverse lamina extends caudally, it tilts to a 45° angle to the palate to nearly parallel to the nasal septum. All of the marsupials I examined with a maxillary recess have the medial wall of the recess at least partially formed by the posterior transverse lamina. In most cases the entire medial wall of the recess is formed by the transverse lamina.

Cribriform Plate

The cribriform plate is a paired structure, each representing the coalescence of the

caudal portions of the nasoturbinal, endoturbinals, and ectoturbinals from each half of the nasal cavity (Allen, 1882; Rowe et al., 2005; fig. 5). The posterior transverse lamina also contributes to the cribriform plate in *Notoryctes*. The two plates are divided medially by the ossified nasal septum, which may project into the endocranial cavity as the crista galli (fig. 23). The cribriform plate is perforated by a number of olfactory foramina that allow passage of bundles of the fibers of the olfactory nerve (fila olfactoria) and a large dorsomedial opening called the *cribroethmoidal foramen* (fig. 23) for passage of the anterior ethmoidal nerve (Wible, 2008).

The cribriform plate as a whole forms a bony partition between the caudalmost extent of the nasal cavity and the rostral border of the ethmoidal fossae of the endocranial cavity, which houses the olfactory bulbs and associated soft tissue structures. The surface

TABLE 4
Number of endoturbinals and ectoturbinals for marsupial species examined

Species	Higher taxon	No. Endo	No. Ecto	Notes
<i>Caluromys philander</i>	Didelphidae	5	2	
<i>Didelphis virginiana</i>	Didelphidae	5	2	
<i>Monodelphis domestica</i> ¹	Didelphidae	5	2	
<i>Caenolestes fuliginosus</i>	Caenolestidae	5	2	
<i>Dasyurus hallucatus</i>	Dasyuridae	5	2	
<i>Sarcophilus lanarius</i>	Dasyuridae	6	4	
<i>Sminthopsis crassicaudata</i>	Dasyuridae	5	2	
<i>Thylacinus cynocephalus</i>	Thylacinidae	5	2	
<i>Notoryctes typhlops</i>	Notoryctidae	5	2/3^a	
<i>Isodon macrourus</i>	Peramelidae	5	2	
<i>Echymipera kalubu</i>	Peramelidae	5	2	
<i>Dromiciops gliroides</i>	Microbiotheriidae	5	2	
<i>Macrotis lagotis</i>	Thylacomyidae	5	2	
<i>Acrobates pygmaeus</i>	Acrobatidae	4	2	
<i>Cercartetus caudatus</i>	Burramyidae	4	2	
<i>Myrmecobius fasciatus</i>	Myrmecobiidae	5	2	
<i>Tarsipes rostratus</i>	Tarsipedidae	3	1	
<i>Petaurus breviceps</i>	Petauridae	5	3	
<i>Petauroides volans</i>	Pseudocheiridae	5	2	
<i>Pseudocheirus occidentalis</i>	Pseudocheiridae	5	2	
<i>Pseudocheirops cupreus</i>	Pseudocheiridae	5	2	
<i>Phalanger orientalis</i>	Phalangeridae	5	3	
<i>Trichosurus vulpecula</i>	Phalangeridae	5	3^b	
<i>Hypsiprymnodon moschatus</i>	Hypsiprymnodontidae	5	3	
<i>Potorous tridactylus</i>	Potoroidae	5	4	
<i>Phascolarctos cinereus</i>	Phascolarctidae	5	1	
<i>Vombatus ursinus</i>	Vombatidae	7	2	
<i>Dendrolagus lumholtzi</i>	Macropodidae	4	2	
<i>Wallabia bicolor</i>	Macropodidae	5	3	

Abbreviations: ¹, specimens examined include TMM M-7599 (Rowe et al., 2005), TMM M-8271, and TMM M-8273; ecto = ectoturbinal; endo = endoturbinal. Differences from the normal marsupial condition of five endoturbinals and two ectoturbinals are indicated in bold text.

^aThis skull of *Notoryctes typhlops* has three ectoturbinals on the right and two on the left.

^bOn the right side of this skull of *Trichosurus vulpecula*, endoturbinal II branches off the turbinal lamella of endoturbinal I, whereas on the left side the lamella of endoturbinal II is attached to the posterior transverse lamina.

of the cribriform plate that faces the endocranial cavity is called the *encranial surface* (Allen, 1882). Generally in mammals, the encranial surface consists of perforate and imperforate portions (Allen, 1882; fig. 23). The perforate portion corresponds with the ectoturbinals, dorsalmost endoturbinals, and the septoturbinal space. The imperforate portion of the encranial surface corresponds with the ventralmost endoturbinals (Allen, 1882).

In marsupials, a vertical column of olfactory foramina are present on both sides of the crista galli on the encranial surface of the cribriform plate (fig. 23). The largest of these foramina,

the cribroethmoidal foramen, is usually closest to the roof of the endocranial cavity (fig. 23). These foramina correspond with the septoturbinal space. Immediately lateral to each column of foramina is an imperforate portion of the cribriform plate. Additional foramina perforate the cribriform plate laterally and ventrally to the imperforate area.

The number and pattern of olfactory foramina in the cribriform plate is variable between specimens examined in this study, but it is unclear how much of this variation is taxonomic versus individual. Some groups of bats have relatively little intraspecific variation in foramina number (Bhatnagar and

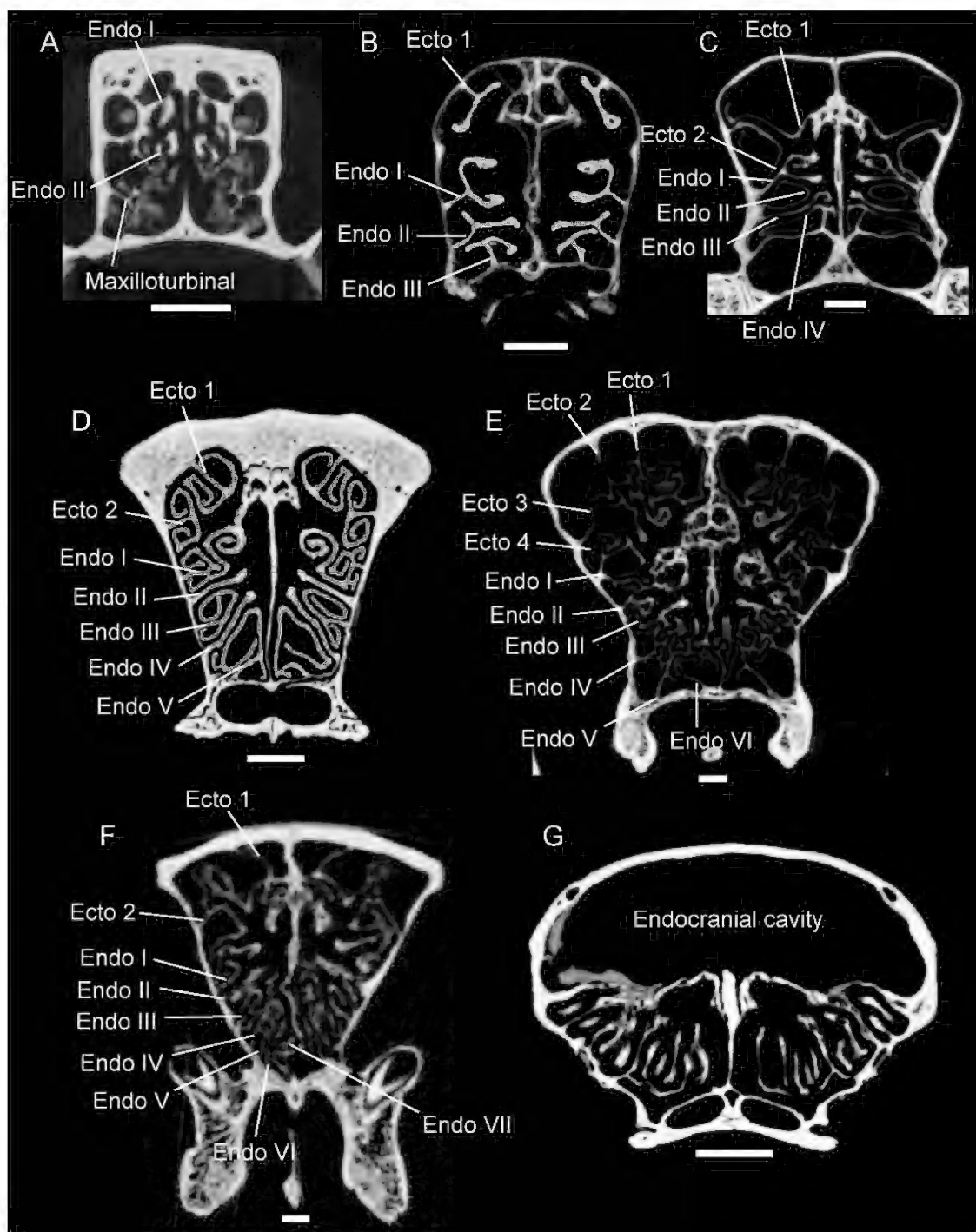


Fig. 18. Coronal CT images showing variation in the number of endoturbinals (char. 18). (A) two endoturbinals present (char. 18.0), *Ornithorhynchus anatinus*, C274 (AMNH 200255), scale bar equals 5 mm; (B) three endoturbinals present (char. 18.1), *Tarsipes rostratus*, C449 (AMNH 119717), scale bar equals 1 mm; (C) four endoturbinals present (char. 18.2), *Dendrolagus lumholtzi*, C296 (AMNH 65254), scale bar equals 5 mm; (D) five endoturbinals present (char. 18.3), *Didelphis virginiana*, C464 (TMM M-2517), scale

Kallen, 1974a), but because of small intra-specific sample sizes, individual variation cannot be addressed here for marsupials.

Ossified Nasal Septum

The nasal septum is the division between the right and left chambers of the nasal cavity (fig. 5). This element begins as a cartilaginous structure in the chondrocranium and in postnatal development the caudal two-thirds of the septum ossify via endochondral ossification (Rowe et al., 2005). Ossification proceeds from caudal to rostral, usually beginning ventral to the developing olfactory bulbs of the brain (Broom, 1926).

There is some controversy as to whether the ossification of the nasal septum in marsupials spreads from an ossification center of the presphenoid (Broom, 1926, 1927, 1935), or whether it proceeds from a separate, more rostral ossification center and therefore should be called a mesethmoid (Rowe et al., 2005). Studies in other groups of mammals suggest that a reexamination of the origin of the ossification of the nasal septum is warranted (Ferigolo, 1981). Because such a study was not undertaken here, I simply refer to the structure in adult skulls as an *ossified nasal septum*. I follow Rowe et al. (2005) in recognizing the ossified nasal septum as a separate element from the ethmoid (see appendix 1 for justification).

In adult marsupials, the rostralmost point of ossification of the septum is around the crowns of the upper canines. Rostral to this point, the nasal septum is cartilaginous in the adult. Ventrocaudally, the ossified septum fuses indistinguishably with the sphenoid complex. Dorsocaudally, the crista galli of the ossified nasal septum typically projects a short distance through the cribriform plate into the endocranial cavity. The cartilaginous nasal septum and the rostralmost portion of the ossified nasal septum articulate with a

dorsal groove in the premaxillae. Caudally, the ventral edge of the ossified septum articulates with a V-shaped median groove on the dorsal surface of the vomer (Rowe et al., 2005). The dorsal edge of the ossified nasal septum articulates with the roofing bones of the nasal cavity; the nasals rostrally and the frontals caudally. Often in adult marsupials, it is difficult to distinguish the boundaries between the ossified septum and the skull roofing bones.

The ossified nasal septum is typically a fairly straight, vertically oriented element along its entire length. However, in most marsupial taxa one or more prominent laterally expanded bulges are present within the shaft of the ossified nasal septum (fig. 24).

Frontal Recess/Sinus

All the marsupial taxa I examined have either a frontal recess or frontal sinus in their nasal cavity. The frontal recess is the dorso-caudal portion of the lateral recess, which is bounded ventrally by the root of endoturbinale I (Maier, 1993a; Rossie, 2006; fig. 8). In adult skulls, the frontal recess is located caudal to the division of the medial wall of the lateral recess (the nasoturbinale) around the root of endoturbinale I. The frontal recess or sinus houses the ectoturbinals (fig. 25).

If secondary pneumatization occurs ontogenetically in the frontal bone surrounding the recess, this space becomes known as the frontal sinus (Rossie, 2006). I do not have an appropriate sample size to examine the development of the frontal recess in the marsupial taxa examined. I used ontogenetic data from the literature when available, but otherwise had only a single adult skull to examine for many taxa. In these cases, I refer to particularly widely expanded spaces that are bound by bone on all sides (in coronal section) as frontal sinuses. Future examination of the development of these taxa might

←

bar equals 5 mm; (E) six endoturbinals present (char. 18.4), *Sarcophilus lanianus*, C323 (USNM 307639), scale bar equals 5 mm; (F) seven endoturbinals present (char. 18.5), *Vombatus ursinus*, C219 (TMM M-2953), scale bar equals 5 mm; (G) more than seven endoturbinals present (char. 18.6), *Tachyglossus aculeatus*, C419 (AMNH 154457), scale bar equals 5 mm. Note: it is not possible to show all of the endoturbinals of *Tachyglossus* in a single coronal slice. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal.

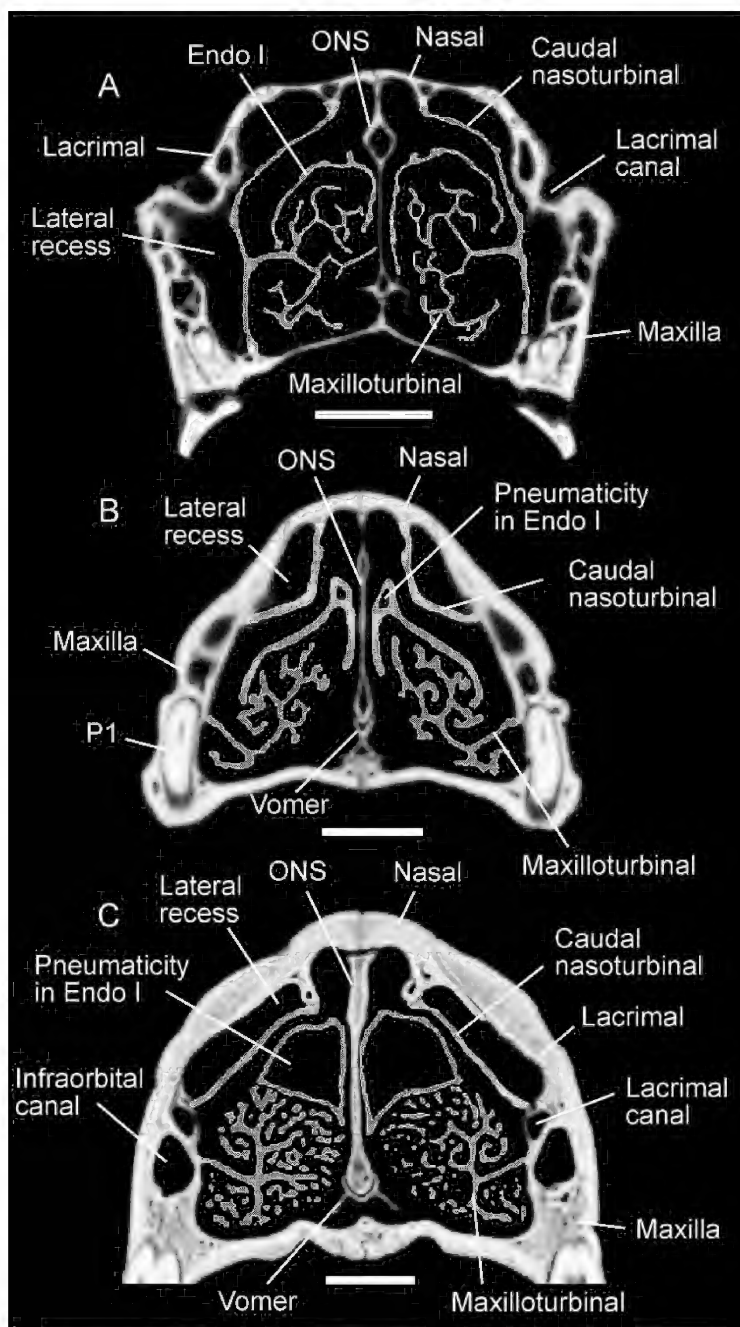


Fig. 19. Coronal CT images showing pneumaticity of the rostral portion of endoturbinal I (char. 17). (A) rostral portion contains no pneumatic cavities (char. 17.0), *Petauroides volans*, C370 (AMNH 150055); (B) small pneumatic cavity is present, which encompasses only a portion of the coronal cross section of the element (char. 17.1), *Phalanger orientalis*, C160 (AMNH 157211); (C) large cavity is present, which encompasses most or the entire coronal cross section of the element (char. 17.2), *Didelphis virginiana*, C270 (TMM M-2517). All scale bars equal 5 mm. Abbreviations: Endo, endoturbinal; ONS, ossified nasal septum; P1, first upper premolar.

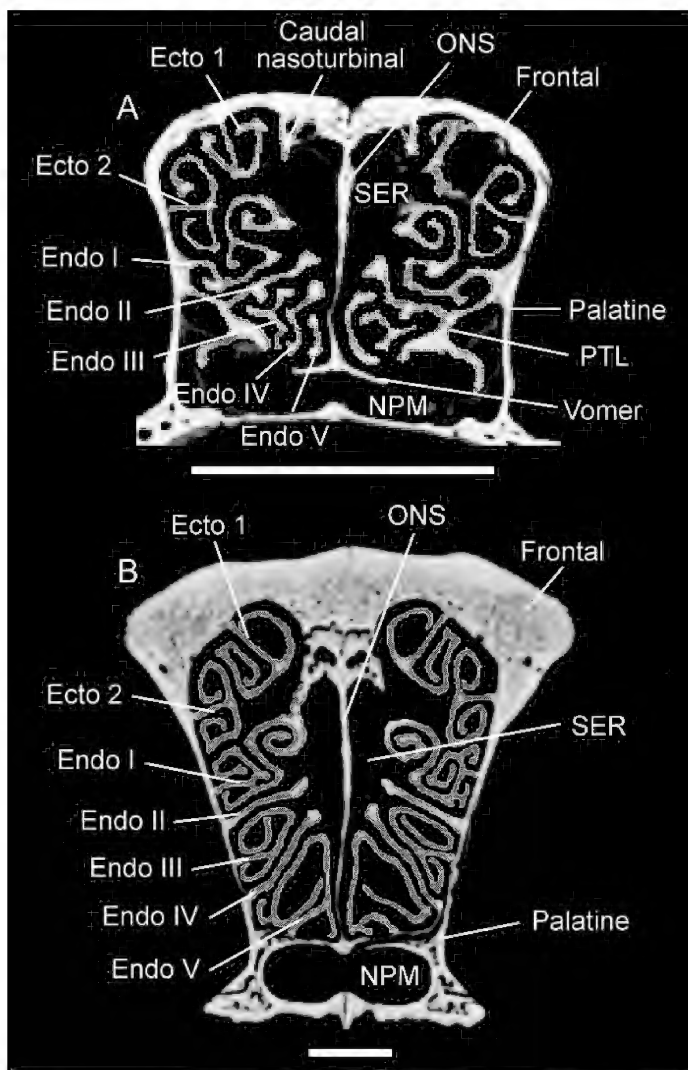


Fig. 20. Coronal CT images showing the number of turbinal folds on endoturbinal I (char. 15). (A) one (ch. 15.1), *Monodelphis domestica*, C205 (TMM M-7599); (B) two (ch. 15.2), *Didelphis virginiana*, C464 (TMM M-2517). All scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; NPM, nasopharyngeal meatus; ONS, ossified nasal septum; PTL, posterior transverse lamina; SER, sphenethmoid recess.

suggest that these spaces are actually recesses and not sinuses. But the majority of marsupials I examined have a frontal recess rather than a frontal sinus.

Maxillary Recess/Sinus

The maxillary recess is the ventrocaudal portion of the lateral recess that is bounded

dorsally by the root of endoturbinal I. Secondary pneumatization of this space results in a maxillary sinus (Rossie, 2006). Many but not all of the marsupials I examined have a maxillary recess (fig. 26), but none of these are particularly expanded, which suggests that the spaces are not maxillary sinuses. Again, I do not have the sample sizes to rigorously determine whether

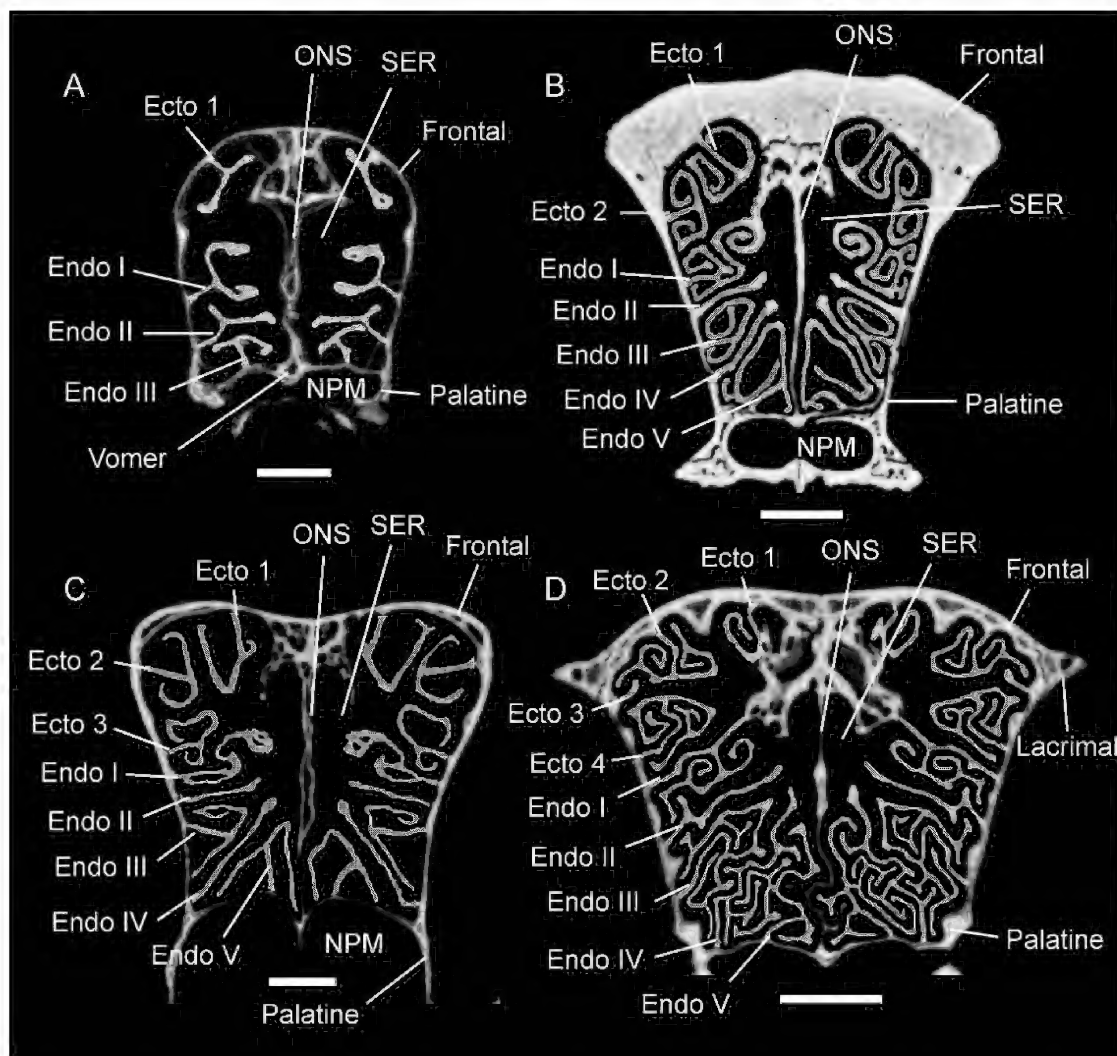


Fig. 21. Coronal CT images showing variation in the number of ectoturbinals (char. 19). (A) one ectoturbinal is present (char. 19.0), *Tarsipes rostratus*, C449 (AMNH 119717), scale bar equals 1 mm; (B) two ectoturbinals (char. 19.1), *Didelphis virginiana*, C464 (TMM M-2517), scale bar equals 5 mm; (C) three ectoturbinals (char. 19.2), *Wallabia bicolor*, C430 (TMM M-4169), scale bar equals 5 mm; (D) four ectoturbinals (char. 19.3) *Potorous tridactylus*, C495 (AMNH 65337), scale bar equals 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; NPM, nasopharyngeal meatus; ONS, ossified nasal septum; SER, sphenethmoid recess.

secondary pneumatization occurs during the development of the maxillary recess. But I have seen no evidence for a maxillary sinus in a marsupial.

In the majority of marsupials with a maxillary recess, the posterior transverse lamina is the only element forming the medial boundary of the recess (fig. 27). The uncinate process of the caudal nasoturbinal also

contributes to this medial border of the recess in a few taxa (fig. 27).

Taxonomic Variation from Generalized Marsupial Condition

Below I describe taxonomic variation from the generalized marsupial condition of the ethmoid described above. Taxonomic

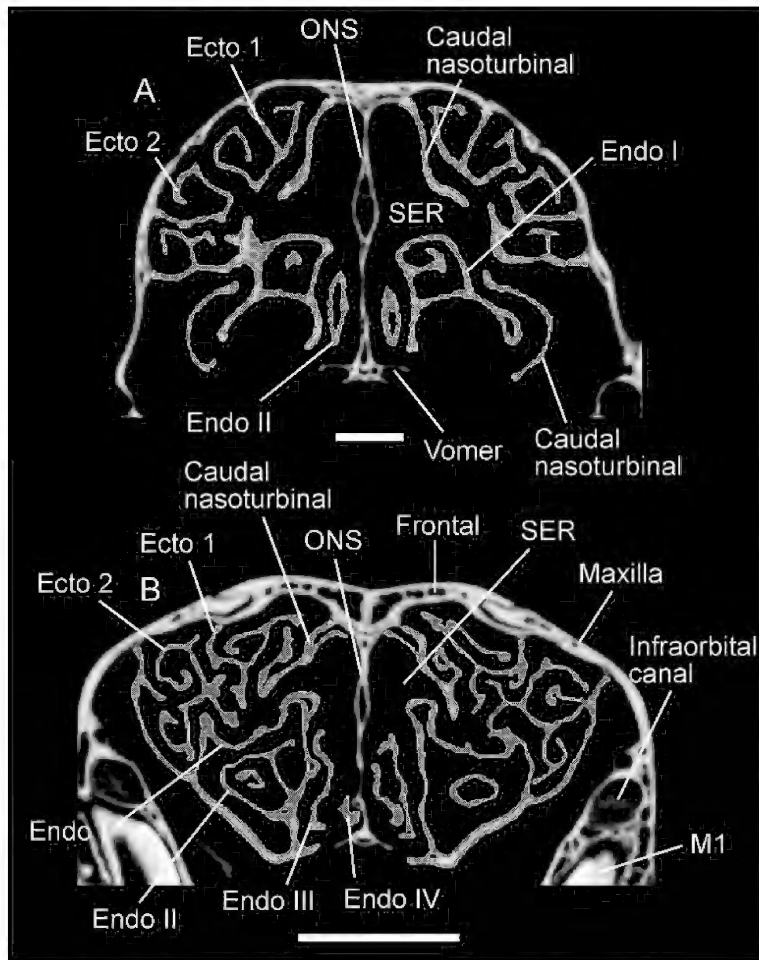


Fig. 22. Coronal CT images showing the morphology of the rostral portion of ventralmost ectoturbinal (char. 22). (A) lamella does not contact posterior transverse lamina (char. 22.0), *Dromiciops gliroides*, C245 (FMNH 127463); (B) lamella is attached to posterior transverse lamina (char. 22.1), *Macroctis lagotis*, C485 (AMNH 74486). Both scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; M1, first upper molar; ONS, ossified nasal septum; SER, sphenethmoid recess.

variation is examined for family-level clades of marsupials. The number of turbinal elements for each species examined is reported in table 4 and the CT slice numbers for which each element is visible in the coronal plane is reported in table 5.

DIDELPHIDAE: I examined *Caluromys philander*, *Didelphis virginiana*, and *Monodelphis domestica* as representatives of the clade Didelphidae, which includes 91 extant species distributed across 18 genera (Voss and Jansa, 2009). The rostral maxilloturbinal of *Monodelphis* observed in the coronal plane through the rostral portion of the roots of the upper

canines is a single scroll unlike the arborlike maxilloturbinals present in the other two didelphids and the majority of marsupials I examined (fig. 28). The rostralmost attachment of the maxilloturbinal to the lateral wall of the nasal cavity is rostral to the rostralmost portion of the upper canine roots in *Caluromys* and *Monodelphis*, but the maxilloturbinal attachment is even with the canine roots in *Didelphis*.

Both *Monodelphis* and *Caluromys* lack an ossified rostral nasoturbinal contra the condition in *Didelphis* and most other marsupials I examined. The rostral nasoturbinal in

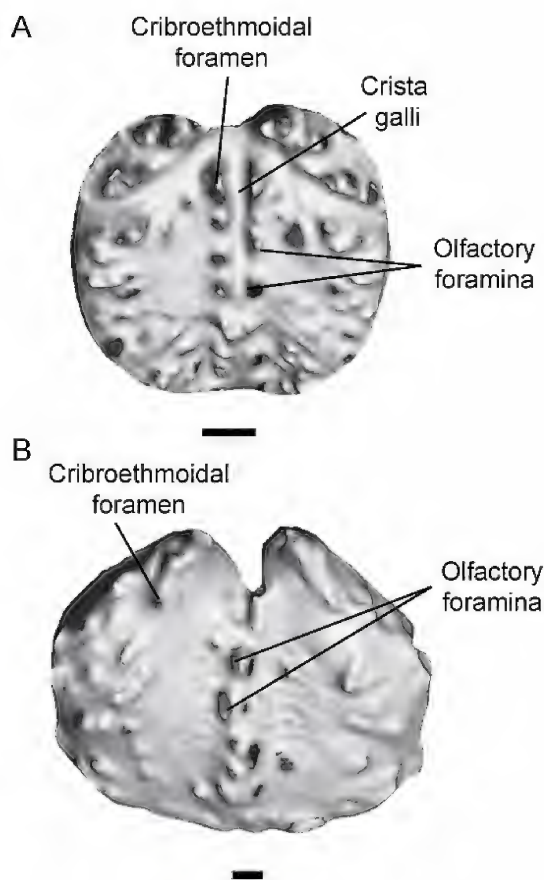


Fig. 23. Digital renderings of the cribriform plate showing the presence or absence of a crista galli (char. 34). (A) crista galli is present (char. 34.0), *Caluromys philander* (AMNH 95526); (B) crista galli is absent (char. 34.1), *Dendrolagus lumholtzi* (AMNH 65254). Both scale bars equal 1 mm.

Didelphis is a small, robust process with a ventromedial inflection. However, in all three didelphid species endoturbinale I projects more rostrally in the skull than the nasoturbinal (fig. 5). The rostral portions of the caudal nasoturbinals of the three didelphids are straight and oriented parallel to the portion of the maxilla forming the nasal cavity lateral wall (fig. 11) and at an oblique angle to the ossified nasal septum. This is contrary to the condition present in the majority of marsupials I examined. The dorsal portion of the nasoturbinal caudal to its division around endoturbinale I is curled in *Caluromys* (C221–237) contra the unfolded morphology present in the other didelphids

and the majority of marsupials. The uncinate process of all three didelphids is present as an ossified structure contra the most common condition in marsupials. The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the lacrimal canal in *Didelphis* and the lateral wall of the nasal cavity in *Monodelphis* and *Caluromys*. The caudalmost extent of the ventral attachment of the nasoturbinal is rostral to the caudal terminus of the maxilloturbinal in *Didelphis*, even with the terminus of the maxilloturbinal in *Caluromys*, and caudal to the maxilloturbinal terminus in *Monodelphis*.

I report five endoturbinals and two ectoturbinals for all three didelphid species examined (table 4). This number of elements corroborates what Freyer (1999) reports for adult *Didelphis marsupialis* and *Monodelphis domestica* (table 3). However, Paulli (1900a) reports four endoturbinals and four ectoturbinals for *Didelphis virginiana*. The fourth ectoturbinal of Paulli (1900a) corresponds with the element that I name *endoturbinale III* in *D. virginiana*. The third ectoturbinal of Paulli may correspond with a turbinal lobe of endoturbinale I.

The rostral portions of endoturbinale I of all three didelphids have pneumatic cavities similar to the generalized condition for marsupials, but the cavity in *Didelphis* is significantly larger than in the other two species (fig. 19). The caudal portion of endoturbinale I of *Didelphis* has three turbinal folds unlike the condition in the other didelphid species and most marsupials, which is the presence of only one fold (fig. 20). The caudal portion of endoturbinale III of *Caluromys* lacks turbinal folds unlike the element in the other two didelphids and the majority of marsupials, which has two turbinal folds. The rostral portion of endoturbinale IV is branched at its medial terminus in *Didelphis* and sometimes in *Monodelphis* contra the unbranched condition present in *Caluromys* and most other marsupials. The lamella of the caudal portion of endoturbinale V is attached to the lateral wall of the nasal cavity in all three didelphids at the rostralmost point of contribution of the turbinal to the cribriform plate.

The rostral portion of the ventralmost ectoturbinal does not contact the posterior

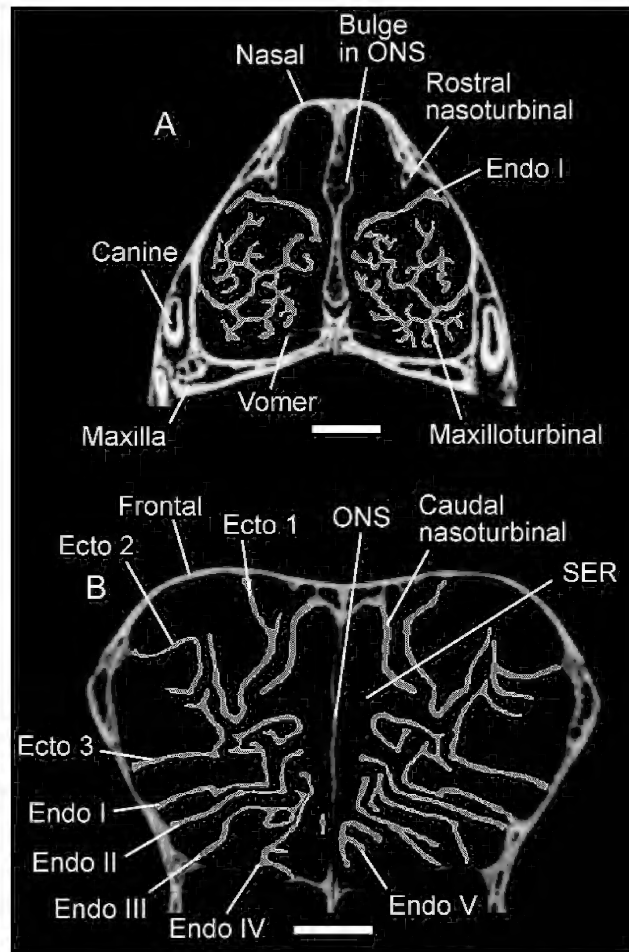


Fig. 24. Coronal CT images showing the presence or absence of prominent lateral expanded bulges within the shaft of the ossified nasal septum (char. 31). (A) bulges present (char. 31.0), *Dromiciops gliroides*, C136 (FMNH 127463), scale bar equals 1 mm; (B) bulges absent (char. 31.1), *Wallabia bicolor*, C386 (TMM M-4169), scale bar equals 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; SER, sphenethmoid recess.

transverse lamina unlike the condition in most marsupials in which this element attaches to the lamina.

The medial wall of the maxillary recess of didelphids is formed by the posterior transverse lamina and the uncinat process (fig. 27). This is a unique condition among marsupials. In other marsupials the medial wall of the maxillary recess is formed exclusively by the posterior transverse lamina (fig. 27).

The cribriform plates of didelphids generally follow the marsupial condition of having a continuous vertical column of olfactory

foramina present on both sides of the crista galli (fig. 23). However, *Monodelphis* deviates from this pattern in that there is a large imperforate region between the cribroethmoidal foramen and the olfactory foramen ventral to it. In addition, the dorsalmost foramen of *Monodelphis* is laterally offset from the midline.

The rostralmost point of ossification of the nasal septum is rostral to the crown of the upper canines in *Caluromys* and some *Monodelphis*, even with the upper canines in other specimens of *Monodelphis*, and caudal to the crown of the upper canines in *Didelphis*. The

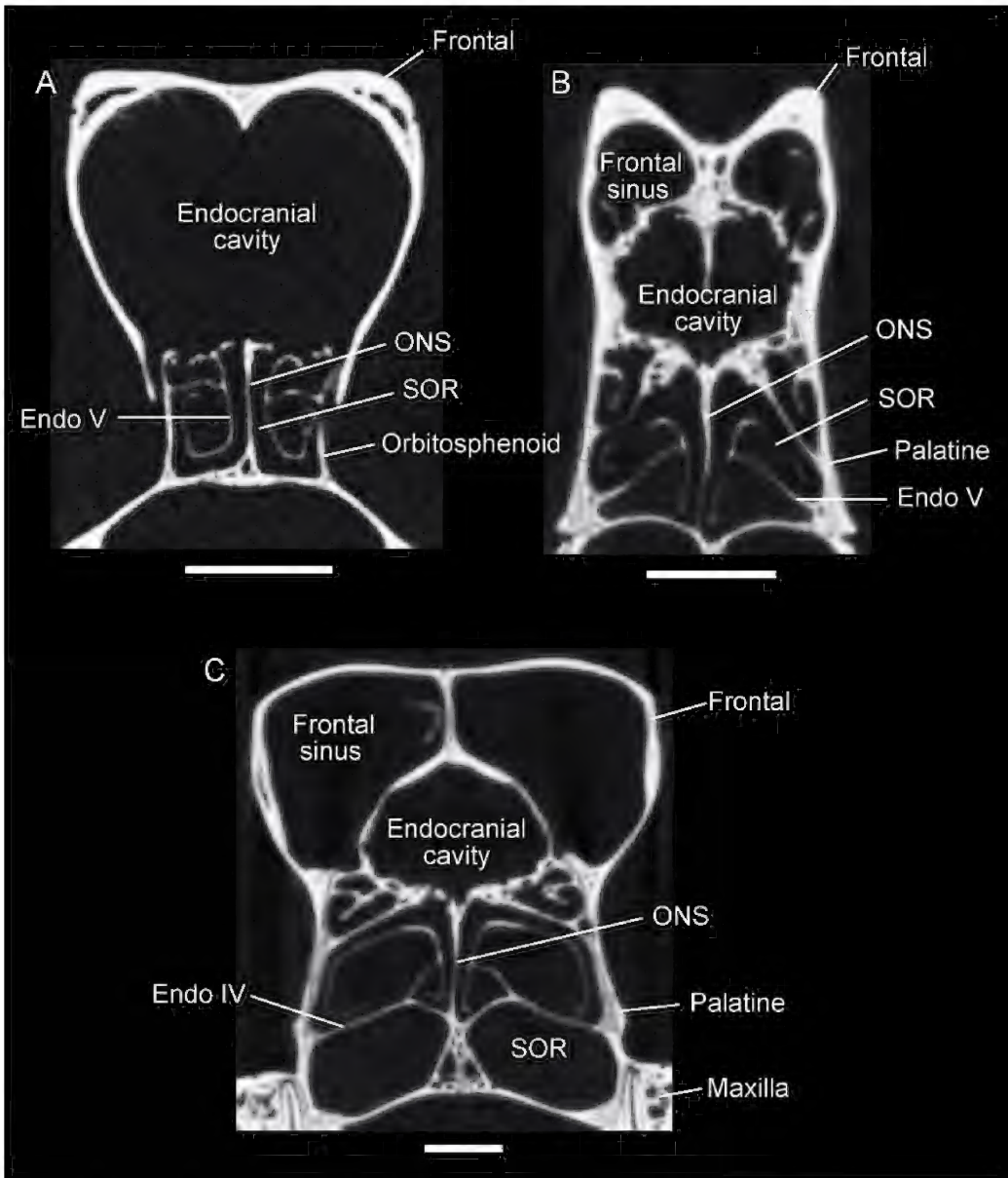


Fig. 25. Coronal CT images showing the presence or absence of a frontal sinus (character 27). (A) no frontal sinus is present (char. 27.0), *Dasyurus hallucatus*, C428 (TMM M-6921); (B) small frontal sinus is present that comprises less than half of the cross sectional area of the frontals (char. 27.1), *Phalanger orientalis*, C342 (AMNH 157211); (C) large frontal sinuses present that comprises most or all of the cross sectional area of the frontals (char. 27.2), *Dendrolagus lumholtzi*, C329 (AMNH 65254). All scale bars equal 5 mm. Abbreviations: Endo, endoturbinale; ONS, ossified nasal septum; SOR, sphenoidal recess.

presence of a crista galli is variable in *Monodelphis*.
CAENOLESTIDAE: *Caenolestes fuliginosus* is the representative I examined from this clade, which includes six extant species

distributed in three genera (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is rostral to the rostralmost portion of the roots of the upper canines. According to Osgood (1921), the

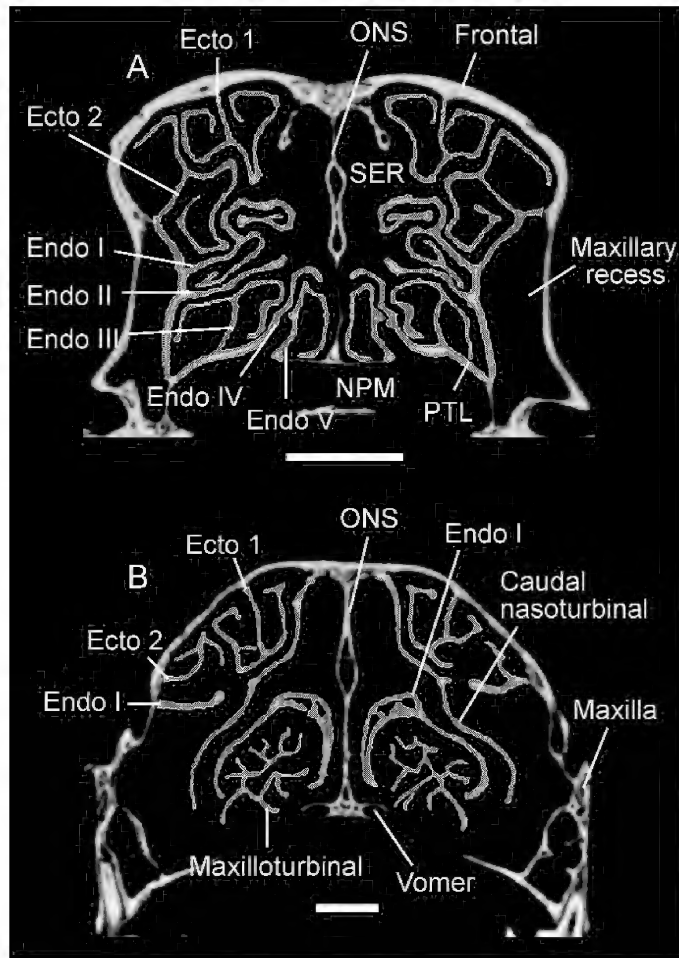


Fig. 26. Coronal CT images showing the presence or absence of a maxillary recess (char. 25). (A) recess is present (char. 25.0), *Dasyurus hallucatus*, C330 (TMM M-6921), scale bar equals 5 mm; (B) recess is absent (char. 25.1), *Dromiciops gliroides*, C230 (FMNH 127463), scale bar equals 1 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; NPM, nasopharyngeal meatus; PTL, posterior transverse lamina; SER, sphenethmoid recess.

maxilloturbinal of *Caenolestes* attaches to the nasal wall at a higher level than in polyprotodonts, and is not largely enclosed by the rostral portion of endoturbinal I, as in diprotodonts.

The rostral nasoturbinal is a slender, ventromedially directed bony process in *Caenolestes*. The caudal nasoturbinal has a laterally projecting turbinal branch that bifurcates into two turbinal lobes (fig. 12; C376–410). The morphology of this projection resembles an ectoturbinal. The rostrodorsal and rostroventral portions of the

caudal nasoturbinal are kinked at nearly a right angle to each other. The uncinat process is present as an ossified structure in *Caenolestes* contra the condition in most marsupials. The caudalmost point of ventral attachment of the nasoturbinal is on the floor of the nasal cavity, unlike the condition in most marsupials (fig. 15).

I report five endoturbinals and two ectoturbinals for *Caenolestes* (table 4). In contrast only four endoturbinals are reported by Osgood based on a midsagittal section (Osgood, 1921: plate XVII). The sagittal view

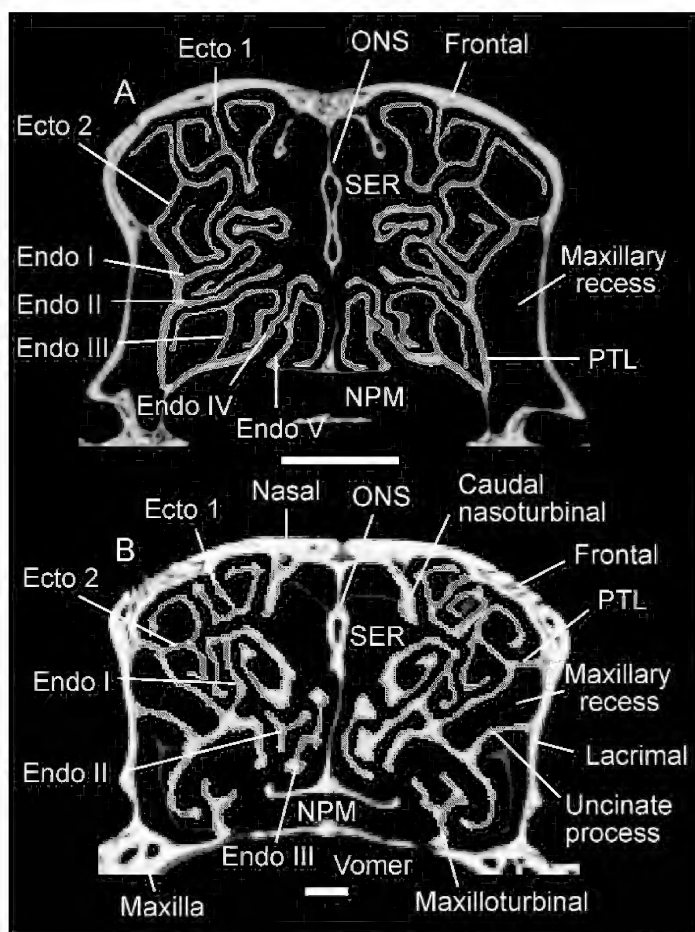


Fig. 27. Coronal CT images showing the morphology of the maxillary recess (char. 26). (A) caudal portion of recess is medially enclosed by posterior transverse lamina (char. 26.0), *Dasyurus hallucatus*, C330 (TMM M-6921), scale bar equals 5 mm; (B) uncinat process of the caudal nasoturbinal also contributes to the medial wall of the recess (char. 26.1), *Monodelphis domestica*, C190 (TMM M-7599), scale bar equals 1 mm. Abbreviation: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; NPM, nasopharyngeal meatus; PTL, posterior transverse lamina; SER, sphenethmoid recess.

often does not show endoturbinal III, and this may explain the discrepancy in the number of endoturbinals.

Endoturbinal I of *Caenolestes* is relatively short compared to other taxa, extending forward only to the coronal plane of the anterior portion of P3; this is similar to the condition in *Trichosurus* and *Petaurus* (Osgood, 1921). In contrast, endoturbinal I in didelphids and *Phascologale* is very long, reaching as far anterior as the canines and almost completely enclosing the fenestrated part of the maxilloturbinal (Osgood, 1921).

The rostral portion of endoturbinal I of *Caenolestes* lacks any pneumatic vacuities. The caudal portion of endoturbinal I has three turbinal folds rather than one, which is the condition in most marsupials. The lamella of endoturbinal V is attached to the floor of the nasal cavity at the rostralmost point of contribution of the turbinal to the cribriform plate. At this point, the turbinal folds of endoturbinal V are asymmetrical in size.

Endoturbinal V of *Caenolestes* is reportedly relatively larger than in other taxa and is

closest in form to *Perameles nasuta* (Osgood, 1921).

The rostral portion of the lamella of the ventralmost ectoturbinal in *Caenolestes* does not contact the posterior transverse lamina contrary to the condition in most marsupials.

The cribriform plate of *Caenolestes* is reportedly more upright than in didelphids and resembles that of *Perameles* (Osgood, 1921). Also, the cribriform plate of *Caenolestes* has a vertical column of olfactory foramina on each side of the crista galli, but the columns are not continuous. There is a large imperforate region between the cribroethmoidal foramen and the olfactory foramen immediately ventral. In addition, the dorsalmost foramen is laterally offset from the crista galli.

The rostral extent of the ossified nasal septum is rostral to the crowns of the upper canines (fig. 29).

MICROBIOTHEREIIDAE: I examined CT imagery of a skull of *Dromiciops gliroides*, the only extant microbiothere (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is rostral to the rostralmost portion of the roots of the upper canines.

The rostral nasoturbinal is present in *Dromiciops* as a small, robust bony process with a ventromedial inflection. However, endoturbinal I projects more rostrally in the skull than the nasoturbinal. The rostral portion of the caudal nasal turbinal of *Dromiciops* has a kinked morphology such that its rostradorsal and rostroventral portions are oriented at nearly a right angle to each other. Caudal to this, the caudal nasoturbinal contains pneumatic vacuities (C232–238) and the caudalmost point of ventral attachment of the nasoturbinal is on the lateral wall of the nasal cavity and rostral to the caudal terminus of the maxilloturbinal. An ossified uncinat process of the nasoturbinal is absent.

Dromiciops has the typical marsupial number of five endoturbinals and two ectoturbinals (table 4).

The caudal portion of endoturbinal I of *Dromiciops* has three turbinal folds and four turbinal lobes that branch from the lamella. This is contrary to the typical marsupial

condition of one turbinal fold and three turbinal lobes. The lamella of endoturbinal V is attached to the lateral wall of the nasal cavity at the rostralmost point of contribution of this turbinal to the cribriform plate. At this point, the turbinal folds of endoturbinal V are asymmetrical in size.

The ventralmost ectoturbinal does not bifurcate at the rostralmost point of contribution of this element to the cribriform plate. The lamella of the ventralmost ectoturbinal does not contact the posterior transverse lamina contrary to the condition in most marsupials (fig. 22).

The cribriform plate of *Dromiciops* has a vertical column of olfactory foramina on each side of the crista galli, but the columns are not continuous. There is a large imperforate region between the cribroethmoidal foramen and the olfactory foramen immediately ventral. In addition, the dorsalmost foramen is laterally offset from the crista galli.

The rostralmost point of ossification of the nasal septum in *Dromiciops* is even with the crowns of the upper canines (fig. 29). There are prominent lateral expanded bulges within the shaft of the ossified nasal septum (fig. 24). *Dromiciops* lacks a maxillary recess (fig. 26).

DASYURIDAE: I examined *Dasyurus hallucatus*, *Sarcophilus laniarius*, and *Sminthopsis crassicaudata* as representatives of the clade Dasyuridae, which includes 69 extant species distributed in 20 genera (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is rostral to the rostralmost portion of the roots of the upper canines in *Dasyurus* and *Sminthopsis*, but even with the roots in *Sarcophilus*.

The rostral nasoturbinal is present in all three dasyurids as a slender ventromedially directed bony structure (figs. 9 and 10). The rostral portion of the caudal nasoturbinal of *Sarcophilus* and *Sminthopsis* is straight, the general condition for marsupials. However, the rostral portion of the caudal nasoturbinal is distinctive in *Dasyurus*; the dorsal portion is in the shape of a boomerang with the ends oriented dorsally and ventrolaterally, and the ventral portion is curved with the convex surface facing the lateral recess (fig. 11; C204–210). Caudal to this, the caudal

TABLE 5
Extent of turbinal elements in the CT images of marsupial skulls in the coronal plane

Species	Turbinal elements
<i>Acrobates pygmaeus</i>	MT: C106-324; NT: C240-348; EC 1: C297-373; EC 2: C319-388; EN I: C187-394; EN II: C294-406; EN III: C332-428; EN IV: C350-463
<i>Caenolestes fuliginosus</i>	MT: C045-390; NT: C088-452; EC 1: C365-486; EC 2: C371-494; EN I: C385-508; EN II: C391-496; EN III: C441-533; EN IV: C422-544; EN V: C455-576
<i>Caluromys philander</i>	MT: C039-300; NT: C145-310; EC 1: C230-364; EC 2: C235-363; EN I: C079-360; EN II: C239-369; EN III: C288-391; EN IV: C278-400; EN V: C304-443
<i>Cercartetus caudatus</i>	MT: C027-262; NT: C181-311; EC 1: C227-327; EC 2: C237-329; EN I: C098-331; EN II: C233-350; EN III: C266-359; EN IV: C296-388
<i>Dasyurus hallucatus</i>	MT: C041-293; NT: C072-355; EC 1: C274-416; EC 2: C291-414; EN I: C108-377; EN II: C218-380; EN III: C277-421; EN IV: C240-425; EN V: C293-467
<i>Dendrolagus lumholtzi</i>	MT: C057-239; NT: C132-298; EC 1: C183-307; EC 2: C226-316; EN I: C200-331; EN II: C252-332; EN III: C272-339; EN IV: C262-356
<i>Didelphis virginiana</i>	MT: C058-349; NT: C253-460; EC 1: C351-525; EC 2: C351-514; EN I: C213-507; EN II: C329-512; EN III: C378-518; EN IV: C336-522; EN V: C366-565
<i>Dromiciops gliroides</i>	MT: C037-241; NT: C162-287; EC 1: C213-300; EC 2: C220-312; EN I: C093-314; EN II: C237-320; EN III: C283-349; EN IV: C273-356; EN V: C298-393
<i>Echymipera kalubu</i>	MT: C097-422; NT: C291-521; EC 1: C451-619; EC 2: C460-625; EN I: C250-613; EN II: C396-608; EN III: C481-646; EN IV: C451-655; EN V: C511-683
<i>Hypsiprymnodon moschatus</i>	MT: C066-333; NT: C229-379; EC 1: C299-425; EC 2: C312-436; EC 3: C335-438; EN I: C157-439; EN II: C306-445; EN III: C333-461; EN IV: C327-469; EN V: C338-488
<i>Isodon macrourus</i>	MT: C022-356; NT: C235-433; EC 1: C356-496; EC 2: C362-518; EN I: C165-511; EN II: C306-508; EN III: C405-541; EN IV: C372-552; EN V: C410-571
<i>Macrootis lagotis</i>	MT: C062-393; NT: C345-539; EC 1: C443-608; EC 2: C454-620; EN I: C297-617; EN II: C411-621; EN III: C510-643; EN IV: C482-654; EN V: C530-708
<i>Monodelphis domestica</i> ¹	MT: C038-196; NT: C125-219; EC 1: C168-237; EC 2: C174-234; EN I: C121-237; EN II: C171-245; EN III: C197-250; EN IV: C192-265; EN V: C203-281
<i>Myrmecobius fasciatus</i>	MT: C019-250; NT: C061-334; EC 1: C248-364; EC 2: C248-380; EN I: C142-386; EN II: C211-361; EN III: C285-398; EN IV: C276-404; EN V: C302-444
<i>Notoryctes typhlops</i>	MT: 079-266; NT: C141-340; EC 1: C227-384; EC 2: C267-389; EC3 (right side only): C285-390; EN I: C147-389; EN II: C246-386; EN III: C304-414; EN IV: C339-427; EN V: C345-443
<i>Petauroides volans</i>	MT: C116-550; NT: C331-546; EC 1: C468-594; EC 2: C475-587; EN I: C218-586; EN II: C484-571; EN III: C508-620; EN VI: C491-628; EN V: C520-688
<i>Petaurus breviceps</i>	MT: C059-180; NT: C107-175; EC 1: C138-188; EC 2: C139-194; EC3: C157-182; EN I: C144-199; EN II: C160-203; EN III: C190-221; EN IV: C176-226; EN V: C183-254
<i>Phalanger orientalis</i>	MT: C040-227; NT: C151-309; EC 1: C240-329; EC 2: C258-338; EC 3: C264-331; EN I: C121-327; EN II: C185-331; EN III: C247-346; EN VI: C246-353; EN V: C264-380
<i>Phascolarctos cinereus</i>	MT: C085-263; NT: C092-309; EC 1: C260-285; EN I: C238-309; EN II: C270-300; EN III: C261-310; EN IV: C291-318; EN V: C279-314
<i>Potorous tridactylus</i>	MT: C062-380; NT: C318-459; EC 1: C371-509; EC 2: C377-529; EC 3: C439-505; EC 4: C379-532; EN I: C266-530; EN II: C362-531; EN III: C406-553; EN VI: C430-551; EN V: C430-567
<i>Pseudocheirus occidentalis</i>	MT: C050-250; NT: C156-312; EC 1: C229-346; EC 2: C303-344; EN I: C120-349; EN II: C220-334; EN III: C271-347; EN IV: C244-352; EN V: C292-384
<i>Pseudochirops cupreus</i>	MT: C096-390; NT: C306-496; EC 1: C408-526; EC 2: C427-526; EN I: C213-537; EN II: C395-547; EN III: C481-587; EN VI: C448-603; EN V: C470-647
<i>Sarcophilus lanarius</i>	MT: C045-193; NT: C071-305; EC 1: C250-341; EC 2: C223-364; EC 3: C303-349; EC 4: C248-351; EN I: C141-344; EN II: C145-342; EN III: C154-344; EN IV: C219-373; EN V: C199-381; EN VI: C300-345.
<i>Sminthopsis crassicaudata</i>	MT: C025-239; NT: C041-274; EC 1: C225-309; EC 2: C229-312; EN I: C115-319; EN II: C210-318; EN III: C265-342; EN IV: C240-350; EN V: C285-374
<i>Tarsipes rostratus</i>	MT: C048-358; NT: C121-440; EC 1: C387-481; EN I: C273-484; EN II: C394-500; EN III: C426-525

TABLE 5
(Continued)

Species	Turbinal elements
<i>Thylacinus cynocephalus</i>	MT: C043-172; NT: C058-269; EC 1: C209-283; EC 2: C213-280; EN I: C136-281; EN II: C177-282; EN III: C225-288; EN IV: C188-288; EN V: C221-304
<i>Trichosurus vulpecula</i>	MT: C027-220; NT: C122-240; EC 1: C189-277; EC 2: C198-276; EC 3: C215-272; EN I: C118-270; EN II (left side only): C187-268; EN III: C266-290; EN IV: C217-293; EN V: C230-327
<i>Vombatus ursinus</i>	MT: C078-178; NT: C096-216; EC 1: C190-228; EC 2: C194-231; EN I: C158-228; EN II: C188-224; EN III: C188-229; EN IV: C200-231; EN V: C193-232; EN VI: C208-235; EN VII: C199-236
<i>Wallabia bicolor</i>	MT: C117-282; NT: C280-442; EC 1: C320-469 EC 2: C320-479; EC 3: C347-472; EN I: C245-464; EN II: C340-463; EN III: C340-473; EN IV: C359-479; EN V: C386-493

Citation of CT images follows convention described in the Materials and Methods section. Extent of turbinal elements based on right side of skull unless otherwise indicated. Abbreviations: ¹, specimen TMM M-7599, data from Rowe et al. (2005); EC, ectoturbinal; EN, endoturbinal; MT, maxilloturbinal; NT, nasoturbinal.

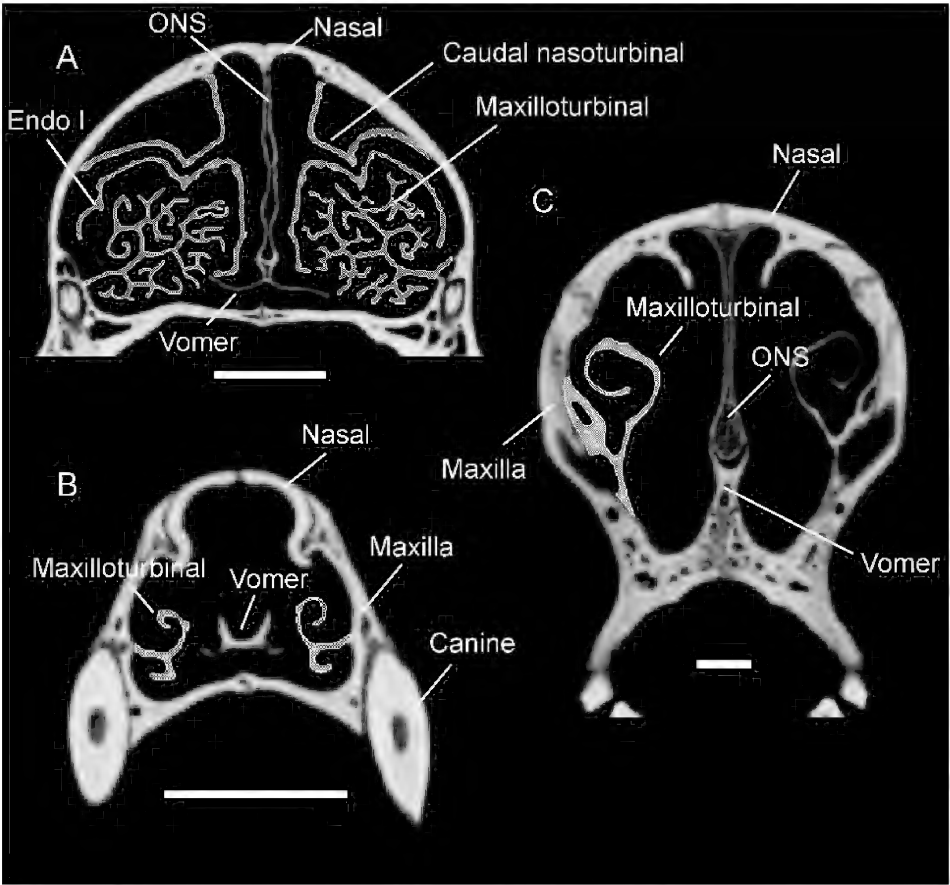


Fig. 28. Coronal CT images showing the complexity of the rostral portion of the maxilloturbinal in marsupials (char. 1). (A) arborlike maxilloturbinal (char. 1.0), *Dasyurus hallucatus*, C208 (TMM M-6921); (B) simple maxilloturbinal (char. 1.1), *Isoodon macrourus*, C150 (TMM M-6922); (C) curled lamella (char. 1.1), *Phascolarctos cinereus*, C129 (TMM M-2946). All scale bars equal 5 mm. Abbreviations: Endo, endoturbinal; ONS, ossified nasal septum.

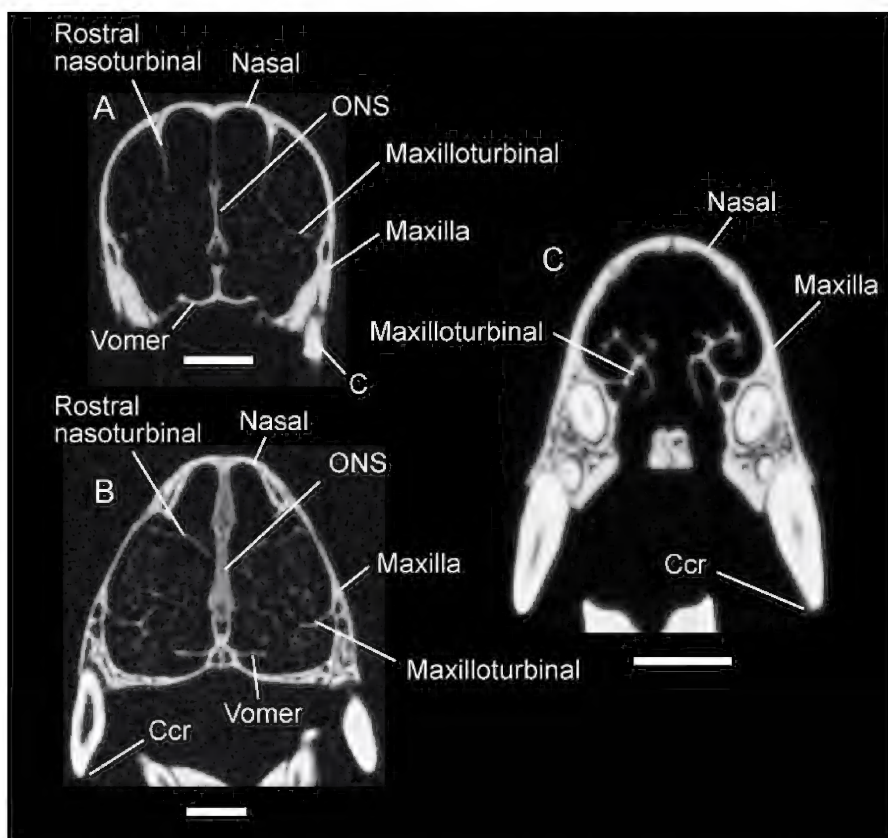


Fig. 29. Coronal CT images showing the rostral extent of ossified nasal septum (char. 29). (A) ossified nasal septum extends rostral to crowns of upper canines (char. 29.0), *Caenolestes fuliginosus*, C136 (KU 124015), scale bar equals 1 mm; (B) septum rostral extent is even with crowns of upper canines (char. 29.1), *Dromiciops gliroides*, C112 (FMNH 127463), scale bar equals 1 mm; (C) septum rostral extent is caudal to crowns of upper canines (char. 29.2), *Phalanger orientalis*, C066 (AMNH 157211), scale bar equals 5 mm. Abbreviations: C, upper canine; Ccr, upper canine crown; ONS, ossified nasal septum.

nasoturbinal of *Dasyurus* and *Sminthopsis* is unbranched, but in *Sarcophilus* two branches project laterally from the nasoturbinal (C247–266). The nasoturbinal of *Dasyercus cristicauda* is apparently also simple, without any bifurcations (Wood Jones, 1949). The caudal nasoturbinal has pneumatic vacuities in *Dasyurus* (C289–296) and *Sarcophilus* (C236–257), but no vacuities are present in *Sminthopsis*. The dorsal portion of the nasoturbinal caudal to its division around endoturbinal I is curled in *Dasyurus* (C290–302) and *Sarcophilus* (C230–304), but the caudodorsal portion is unfolded in *Sminthopsis*. An ossified uncinat process of the nasoturbinal is absent in all three taxa. The

caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the infraorbital canal (V_2) in *Dasyurus* (fig. 15) and *Sarcophilus*, and on the medial wall of the lacrimal canal in *Sminthopsis*. The caudalmost extent of the ventral attachment of the nasoturbinal is rostral to the caudal terminus of the maxilloturbinal in *Sminthopsis*, at the coronal level of the terminus in *Dasyurus*, and caudal to the caudal terminus of the maxilloturbinal in *Sarcophilus*.

The dasyurids I examined have five or six endoturbinals and two or four ectoturbinals (table 4). *Sarcophilus* has the largest number of turbinal elements of any marsupial examined thus far with six endoturbinals and four

ectoturbinals (fig. 18). In contrast to my findings only four endoturbinals are reported for the dasyurids *Dasyercus cristicauda*, *Dasyurus* sp., and *Phascogale* sp. (Wood Jones, 1949). Similarly, only four endoturbinals are described for *Dasyurus viverrinus* (Paulli, 1900a). Perhaps the specimen preparations of these older studies did not allow the authors to see all the endoturbinals in the dasyurids they examined. Alternatively, these reported differences may represent intrataxonomic variation in the number of endoturbinals in Dasyuridae, because I did not examine the same species as the previous studies.

The endoturbinals and ectoturbinals of *Sarcophilus* are convoluted elements that are densely packed creating a tight maze-like pattern in the nasal cavity (fig. 18). In contrast these elements in *Dasyurus* and *Sminthopsis* are not as densely packed and are not convoluted.

The rostral portion of endoturbinal I of *Sarcophilus* is devoid of pneumatic vacuities, whereas there is a small cavity in this element in *Sminthopsis* and a large cavity is present in *Dasyurus*. The caudal portion of endoturbinal I of *Dasyurus* and *Sminthopsis* has two turbinal lobes and in *Sarcophilus* there are three. Endoturbinal I of *Sarcophilus* has three separate lamellae branching from the posterior transverse lamina. Endoturbinal II of *Sarcophilus* is branched at its medial terminus unlike the unbranched morphology present for this element in *Dasyurus*, *Sminthopsis*, and many other marsupials. The lamella of endoturbinal II of *Dasyurus* is attached to the posterior transverse lamina rostrally (C313–339), but caudally the lamella becomes confluent with the lamella of endoturbinal I (C340–378); this relationship is maintained at the point of contribution of both elements to the cribriform plate. The rostral portion of endoturbinal III in *Sarcophilus* is convoluted with multiple branches as opposed to this turbinal in *Dasyurus*, *Sminthopsis*, and many other marsupials, which is bilaminar in morphology. The rostral portion of endoturbinal IV of *Sarcophilus* is branched at its medial terminus unlike the condition in *Dasyurus*, *Sminthopsis*, and the generalized marsupial morphology. Similarly, the caudal portion of endoturbinal IV of *Sarcophilus* is

branched at its medial terminus contrary to the condition in the other dasyurids and the generalized marsupial morphology. The lamella of endoturbinal V of *Dasyurus* and *Sminthopsis* is attached to the lateral wall of the nasal cavity in the sphenoidal recess, whereas the lamella attaches to the nasal cavity floor in *Sarcophilus*.

Sarcophilus has a sixth endoturbinal that is attached to the floor of the nasal cavity rostrally (left side, C313–318), but caudally its lamella is attached to the ossified nasal septum (left side, C319–330). Caudal to this (e.g., C345), the additional turbinal fuses to the ossified nasal septum and does not provide a contribution to the cribriform plate. The sixth endoturbinal is more conspicuous on the right side of this specimen of *Sarcophilus* (fig. 18; C299–340). The rostral portion of this element has a terminal bifurcation (C317–337), and caudally this turbinal is unilaminar but convoluted (C338–340).

Both *Dasyurus* and *Sminthopsis* have two ectoturbinals, which is the typical number for marsupials, but *Sarcophilus* has four ectoturbinals (fig. 18; table 4).

The caudolateral portion of the transverse lamina in the dasyurids I examined is oriented roughly parallel to the nasal septum.

The cribriform plate of each of the dasyurids I examined has an imperforate area above the cribroethmoidal foramen in the column of olfactory foramina aligning the medial edge of the plate. In *Sminthopsis* and *Sarcophilus*, there is a very large cribroethmoidal foramen at the top of the column of olfactory foramina; this is more ventrally located than in other marsupials examined in this study. In addition, there is an imperforate area between the cribroethmoidal foramen and the endocranial cavity roof in all three taxa.

The rostralmost extent of ossification of the nasal septum is caudal to the crowns of the upper canines in the three dasyurids I examined. *Sminthopsis* lacks a crista galli, whereas the other two dasyurids have one.

Sarcophilus has a small frontal sinus, whereas the other dasyurids have only frontal recesses (fig. 25).

THYLACINIDAE: There are no extant members of this clade, but I examined CT imagery

of a skull of the extinct species *Thylacinus cynocephalus*. The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity in the same coronal section through the rostral portion of the roots of the upper canines.

The rostral nasoturbinal of *Thylacinus* is present as a slender, ventromedially directed process. The rostradorsal and rostrocaudal portions of the caudal nasoturbinal are kinked at an acute angle to each other. The caudodorsal portion of the caudal nasoturbinal is curled (C205–225) posterior to the division of the nasoturbinal around the lamella of endoturbinal I. An ossified uncinat process of the nasoturbinal is present in *Thylacinus*. The caudalmost point of attachment of the nasoturbinal is on the lateral wall of the nasal cavity. The caudalmost extent of the ventral attachment of the nasoturbinal is caudal to the caudal terminus of the maxilloturbinal.

Thylacinus has the typical marsupial number of five endoturbinals and two ectoturbinals (table 4). The endoturbinals and ectoturbinals of *Thylacinus* are convoluted elements that are densely packed, creating a tight, mazelike pattern in the nasal cavity.

The rostral portion of endoturbinal I of *Thylacinus* lacks pneumatic vacuities, whereas the caudal portion of this element in this taxon has three turbinal folds, a more complex morphology than is present in most marsupials. Endoturbinal II is branched at its medial terminus. The rostral portion of endoturbinal III is convoluted with multiple branches, whereas the caudal portion of this element has the typical two turbinal folds. The rostral portion of endoturbinal IV is branched at its medial terminus, as is the caudal portion of this element. Both of these conditions are contra the typical marsupial morphology for this element. The caudal portion of endoturbinal V of *Thylacinus*, which is sequestered into the sphenoidal recess, has only one turbinal fold and its lamella is attached to the floor of the nasal cavity at the rostralmost point of contribution of the turbinal to the cribriform plate.

The rostral portion of the lamella of the ventralmost ectoturbinal is attached to the posterior transverse lamina. The posterior transverse lamina is oriented nearly parallel

to the nasal septum along its entire rostrocaudal extent.

The cribriform plate of *Thylacinus* has the typical vertical column of olfactory foramina on both sides of the crista galli. However, the foramina are all of similar size, including the cribroethmoidal foramen, and are evenly spaced. There is no lateral offset of the cribroethmoidal foramen from the crista galli.

The rostral extent of ossification of the nasal septum is caudal to the crowns of the upper canines. The ventral portion of the ossified nasal septum of *Thylacinus* is very convoluted (C238–272). Prominent lateral expanded bulges in the shaft of the ossified nasal septum typically found in marsupials are absent in *Thylacinus*.

Thylacinus has a well-developed, large frontal sinus (C289–381) and a maxillary recess (C212–243) with a medial wall formed entirely by the posterior transverse lamina.

NOTORYCTIDAE: I examined CT imagery of a skull of *Notoryctes typhlops* as a representative of this clade, which includes only two extant species belonging to this single genus (Wilson and Reeder, 2005). The rostral portion of the maxilloturbinal of *Notoryctes* has a simple morphology of a lamella with a single bifurcation. The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines.

An ossified rostral nasoturbinal is absent in *Notoryctes*; however, the caudal nasoturbinal projects more rostrally in the skull than endoturbinal I. The rostradorsal and rostrocaudal portions of the caudal nasoturbinal are kinked at an obtuse angle to each other. Proceeding back in the skull, the caudal nasoturbinal has a single laterally projecting turbinal branch (C237–280) and a single pneumatic vacuity is located near the center of the element (C264–309). An ossified uncinat process of the nasoturbinal is absent. The caudalmost point of ventral attachment of the nasoturbinal is on the floor of the nasal cavity. The caudalmost extent of the ventral attachment of the nasoturbinal is rostral to the caudal terminus of the maxilloturbinal.

Notoryctes has five endoturbinals and two or three ectoturbinals (table 4). The right side of the specimen examined in my study has

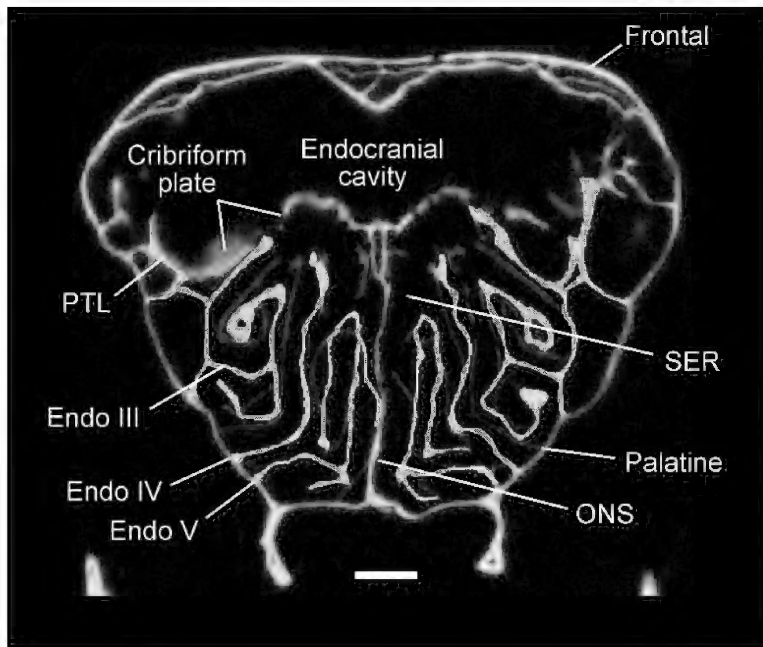


Fig. 30. Coronal CT image showing the contribution of posterior transverse lamina to the cribriform plate (char. state 33.1) shown in *Notoryctes typhlops*, C387 (AMNH 202107). Scale bar equals 1 mm. Abbreviations: Endo, endoturbinale; ONS, ossified nasal septum; PTL, posterior transverse lamina; SER, sphenethmoid recess.

three ectoturbinals, whereas the left side has only two.

The rostral portion of endoturbinale I of *Notoryctes* lacks pneumatic vacuities. The lamella of endoturbinale III is attached to the posterior transverse lamina along its entire length. The lamella of endoturbinale V is attached to the lateral wall of the nasal cavity at the rostralmost point of contribution of the turbinal to the cribriform plate.

The rostral portion of the lamella of the ventralmost ectoturbinal is attached to the posterior transverse lamina.

The posterior transverse lamina of *Notoryctes* contributes to the cribriform plate (fig. 30). This condition does not occur in any other marsupial I have examined.

The endocranial surface of the cribriform plate of *Notoryctes* is similar to the general marsupial condition except that the vertical column of olfactory foramina near the medial edge of the cribriform plate is not continuous. There is a large, imperforate area between the cribroethmoidal foramen and the olfactory foramen immediately ventral. In addition, the cribroethmoidal foramen is

laterally offset from the medial edge of the cribriform plate.

The rostralmost point of ossification of the nasal septum of *Notoryctes* is rostral to the crowns of the upper canines. Caudally, *Notoryctes* lacks a crista galli.

Notoryctes lacks a frontal sinus but possesses a well-developed maxillary recess (C308–401) with a medial wall formed entirely by the posterior transverse lamina. The maxillary recess extends caudally to the point of contribution of the transverse lamina to the cribriform plate.

The caudalmost portion of the sphenoidal recess of *Notoryctes* is laterally restricted by the endocranial cavity (fig. 31). The endocranial cavity surrounds the lateral walls of the nasal cavity at its caudalmost extent (fig. 31; C432–463).

PERAMELIDAE: I examined *Isoodon macrourus* and *Echymipera kalubu* as representatives of this clade, which includes 18 extant species distributed in six genera (Wilson and Reeder, 2005). The rostral maxilloturbinal in both peramelids consists of a lamella with a single bifurcation (fig. 28). The rostralmost

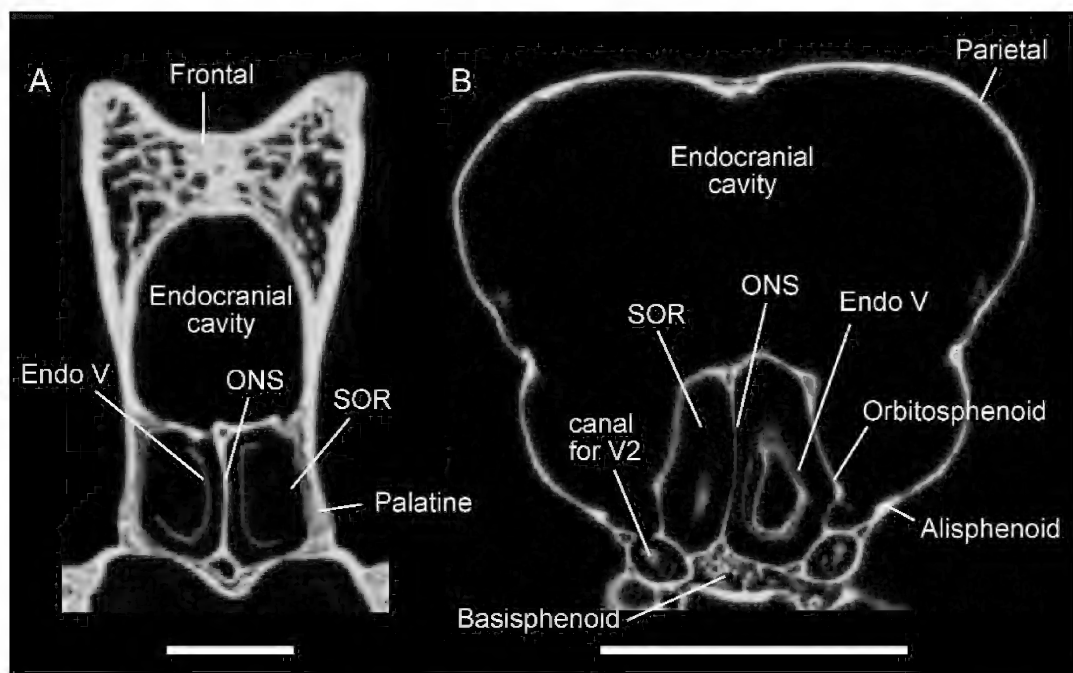


Fig. 31. Coronal CT images showing the morphology of the caudalmost portion of nasal cavity (i.e., sphenoidal recess; char. 35). (A) lateral restriction of sphenoidal recess by the endocranial cavity is absent (char. 35.0), *Trichosurus vulpecula*, C319 (TMM M-849); (B) lateral restriction of sphenoidal recess by the endocranial cavity is present (char. 35.1), *Notoryctes typhlops*, C443 (AMNH 202107). Both scale bars equal 5 mm. Abbreviations: Endo, endoturbinale; ONS, ossified nasal septum; SOR, sphenoidal recess; V2, maxillary branch of trigeminal nerve.

attachment of the maxilloturbinal in both taxa is rostral to the roots of the upper canines.

The rostral nasoturbinal is present in both *Isoodon* and *Echymipera* as a small, robust bony process with a ventromedial inflection. However, endoturbinale I projects more rostrally in the nasal cavity than the nasoturbinal in both taxa. The rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at nearly a right angle in *Isoodon*. The rostral portion of the caudal nasoturbinal in *Echymipera* is similar in morphology to that of *Dasyurus*. The dorsal portion is in the shape of a boomerang with the ends oriented dorsally and ventrolaterally, and the ventral portion is curved with the convex surface facing the lateral recess (C350–400). Caudally, the caudal nasoturbinal of *Isoodon* is unbranched and possesses multiple pneumatic vacuities near the center of the element (C334–425). In contrast, the caudal nasoturbinal of *Echymipera* has a single laterally

projecting turbinal branch (C469–485) and is devoid of pneumatic spaces. Caudal to the division of the nasoturbinal around endoturbinale I, the caudodorsal portion of the nasoturbinal is curled in *Echymipera* (C470–521), whereas this portion of the nasoturbinal remains unfolded in *Isoodon*. An ossified uncinat process of the nasoturbinal is absent in both taxa (fig. 14). The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the lacrimal canal in both taxa (fig. 15). The caudalmost extent of the ventral attachment of the nasoturbinal is posterior to the caudal terminus of the maxilloturbinal in *Isoodon* (fig. 16) and on the right side of the skull of *Echymipera*.

Both peramelids examined here have the typical marsupial number of five endoturbinals and two ectoturbinals (table 4).

The caudal portion of endoturbinale I of peramelids has two turbinal folds and four turbinal lobes. The rostral portion of endoturbinale IV is branched at its medial

terminus in *Echymipera* but unbranched in *Isoodon*. However, the caudal portion of endoturbinale IV is unbranched in both taxa. The lamella of endoturbinale V is attached to the lateral wall of the sphenoidal recess in both peramelid species. At the point of contribution of endoturbinale V to the cribriform plate, the turbinal folds of this element are asymmetrical in size in *Echymipera* but symmetrical in *Isoodon*.

The rostral portion of the lamella of the ventralmost ectoturbinale of *Isoodon* is attached to the posterior transverse lamina, whereas the lamella does not contact the transverse lamina in *Echymipera*.

The encranial surface of the cribriform plate of *Isoodon* and *Echymipera* is similar to the general marsupial condition except that the vertical column of olfactory foramina near the medial edge of the cribriform plate is not continuous. There is a large, imperforate area between the cribroethmoidal foramen and the olfactory foramen immediately ventral. In addition, the cribroethmoidal foramen is laterally offset from the medial edge of the cribriform plate. There is also an imperforate area between the cribroethmoidal foramen and the endocranial cavity roof in *Echymipera*.

The rostralmost point of ossification of the nasal septum is rostral to the crowns of the upper canines in *Echymipera* but caudal to the crowns in *Isoodon*. *Isoodon* and *Echymipera* both lack a crista galli of the nasal septum. Swell bodies are documented at the base of the rostral third of the nasal septum of *Isoodon macrourus* (Kratzing, 1978). Swell bodies regulate whether or not inspired air passes over the maxilloturbinal for warming and humidification (Negus, 1958).

Both peramelid taxa lack a frontal sinus but have a maxillary recess that has its medial wall composed entirely by the posterior transverse lamina.

THYLACOMYIDAE: I examined a specimen of *Macrotis lagotis* as a representative of Thylacomyidae, which includes only two extant species belonging to this single genus (Wilson and Reeder, 2005). The rostral portion of the maxilloturbinal consists of a lamella with a single bifurcation. The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity

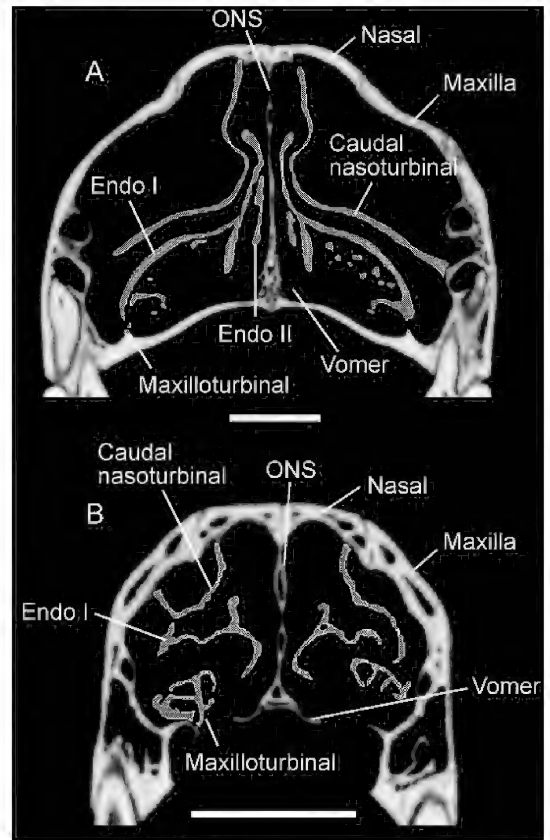


Fig. 32. Coronal CT images showing caudal-most attachment of the maxilloturbinal (char. 3). (A) maxilloturbinal attaches to the floor of the nasal cavity (char. 3.0), *Phalanger orientalis*, C201 (AMNH 157211); (B) maxilloturbinal attaches to the lateral wall of the nasal cavity (char. 3.1), *Macrotis lagotis*, C370 (AMNH 74486). Both scale bars equal 5 mm. Abbreviations: Endo, endoturbinale; ONS, ossified nasal septum.

(fig. 32) rostral to the roots of the upper canines. The caudalmost attachment of the maxilloturbinal is also on the lateral wall of the nasal cavity.

An ossified rostral nasoturbinal is present as a small, robust, ventromedially inflected process. The rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at nearly a right angle to each other. The caudodorsal portion of the nasoturbinal that is posterior to its division around the lamella of endoturbinale I is curled in *Macrotis* (C475–498). The caudal nasoturbinal of *Macrotis* has multiple pneumatic vacuities near the center of the element (C358–405;

C435–499). An ossified uncinat process of the nasoturbinal is absent. The caudalmost point of ventral attachment of the nasoturbinal is posterior to the caudal terminus of the maxilloturbinal on the medial wall of the lacrimal canal.

Macrotis has the typical marsupial number of five endoturbinals and two ectoturbinals (table 4).

The caudal portion of endoturbinal I of *Macrotis* has two turbinal folds and three turbinal lobes. Endoturbinal IV is branched at its medial terminus along nearly its entire rostrocaudal length. The caudal portion of the lamella of endoturbinal V is attached to the lateral wall of the sphenoidal recess. The turbinal folds of endoturbinal V are asymmetrical in size at the point of contribution of this turbinal to the cribriform plate.

The rostral portion of the lamella of the ventralmost ectoturbinal is attached to the posterior transverse lamina (fig. 22). The posterior transverse lamina is oriented nearly parallel to the nasal septum along its entire rostrocaudal length.

The encranial surface of the cribriform plate of *Macrotis* is similar to the general marsupial condition except that the vertical column of olfactory foramina near the medial edge of the cribriform plate is not continuous. There is a large, imperforate area between the cribroethmoidal foramen and the olfactory foramen immediately ventral. In addition, the cribroethmoidal foramen is laterally offset from the medial edge of the cribriform plate.

The rostralmost point of ossification of the nasal septum is caudal to the crowns of the upper canines. The crista galli is absent in *Macrotis*.

Macrotis lacks a frontal sinus but has a maxillary recess, which is bordered medially exclusively by the posterior transverse lamina.

ACROBATIDAE: I examined a specimen of *Acrobates pygmaeus* as a representative of this clade, which includes two extant species distributed in two genera (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines.

The rostral nasoturbinal is present as a short, robust bony process that is ventrome-

dially inflected. The rostral portion of the caudal nasoturbinal is straight and oriented parallel to the portion of the maxilla forming the nasal cavity lateral wall and at an oblique angle to the ossified nasal septum. The caudal nasoturbinal has a single pneumatic vacuity near the center of this element (C313–319). An ossified uncinat process of the nasoturbinal is absent. The caudalmost point of ventral attachment of the nasoturbinal is on the lateral wall of the nasal cavity and rostral to the caudal terminus of the maxilloturbinal.

Acrobates has four endoturbinals and two ectoturbinals (table 4).

The caudal portion of endoturbinal I is simple in morphology; it has only a single bifurcation at the medial terminus and lacks any turbinal folds. Endoturbinal III is bilaminar but lacks turbinal folds. Endoturbinal IV morphologically resembles endoturbinal V of those marsupials with five elements, and its lamella is attached to the lateral wall of the nasal cavity at the rostralmost point of contribution of the turbinal to the cribriform plate.

The rostral portion of the lamella of the ventralmost ectoturbinal is attached to the posterior transverse lamina.

The posterior transverse lamina is oriented at a roughly 45° angle to the orientation of the palate rostrally and caudally it is subparallel to the palate.

The encranial surface of the cribriform plate of *Acrobates* is similar to the general marsupial condition except that the vertical column of olfactory foramina near the medial edge of the cribriform plate is not continuous. There is a large, imperforate area between the cribroethmoidal foramen and the olfactory foramen immediately ventral. In addition, the cribroethmoidal foramen is laterally offset from the medial edge of the cribriform plate.

The rostralmost point of ossification of the nasal septum is in the same coronal plane as the crowns of the upper canines. The crista galli is absent in *Acrobates*.

Acrobates lacks a maxillary recess and a frontal sinus.

BURRAMYIDAE: I examined a specimen of *Cercartetus caudatus* as a representative of Burramyidae, which includes five extant species distributed in two genera (Wilson

and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines. The lamella of the maxilloturbinal is attached to the medial surface of the caudal nasoturbinal, just rostral to the caudal terminus of the maxilloturbinal (C205–210).

The rostral nasoturbinal is absent as an ossified element, and consequently the rostral process of endoturbinal I projects more rostrally in the nasal cavity than the nasoturbinal. The rostral portion of the caudal nasoturbinal is straight and oriented parallel to the portion of the maxilla forming the nasal cavity lateral wall and at an oblique angle to the ossified nasal septum. An ossified uncinat process of the nasoturbinal is absent. The caudalmost point of ventral attachment of the nasoturbinal is on the floor of the nasal cavity and is rostral to the caudal terminus of the maxilloturbinal.

Cercartetus has four endoturbinals and two ectoturbinals (table 4).

Endoturbinals II, III, and IV of *Cercartetus* morphologically resemble endoturbinals III, IV, and V, respectively, of those marsupials with five elements. The lamella of endoturbinal IV is attached to the lateral wall of the sphenoidal recess at the rostralmost point of contribution of the turbinal to the cribriform plate.

The posterior transverse lamina is oriented subparallel to the palate along its entire length. None of the ectoturbinals of *Cercartetus* contacts the posterior transverse lamina.

The cribriform plate of *Cercartetus* has an imperforate area above the dorsalmost foramen in the column of olfactory foramina bordering the medial edge of the plate. The cribroethmoidal foramen is more lateral to the crista galli than in the generalized marsupial condition.

The rostralmost point of ossification of the nasal septum is rostral to the crowns of the upper canines. A crista galli is present.

Cercartetus lacks a maxillary recess and a frontal sinus.

MYRMECOBIIDAE: I examined CT images of a skull of *Myrmecobius fasciatus*, the only extant member of this taxon (Wilson and Reeder, 2005). The rostral maxilloturbinal is simple in morphology, consisting of a lamella

with a single bifurcation. The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines. The caudalmost attachment point of the maxilloturbinal is also on the lateral wall of the nasal cavity.

The rostral nasoturbinal is present as a well-developed, slender, ventromedially directed bony process. The rostral part of the caudal nasoturbinal is straight and oriented parallel to the portion of the maxilla forming the nasal cavity lateral wall and at an oblique angle to the ossified nasal septum. Caudally, the nasoturbinal has a ventrolaterally projecting turbinal branch (C244–259) located on its medial face, and a dorsally projecting turbinal branch (C262–293) on its lateral face. The caudodorsal portion of the nasoturbinal is curled (C259–293) caudal to the division of the nasoturbinal around endoturbinal I. An ossified uncinat process is also present (fig. 14). The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the lacrimal canal. The caudalmost extent of the ventral attachment of the nasoturbinal is posterior to the caudal terminus of the maxilloturbinal.

Myrmecobius has the typical marsupial number of five endoturbinals and two ectoturbinals (table 4).

The rostral portion of endoturbinal I lacks pneumatic cavities. The caudal portion of endoturbinal I has one turbinal fold and five turbinal lobes. The lamella of endoturbinal V is attached to the floor of the nasal cavity at the rostralmost point of contribution of the turbinal to the cribriform plate.

The posterior transverse lamina is oriented nearly parallel to the nasal septum along its entire length. The lamellae of endoturbinals I and II are still attached to the posterior transverse lamina at the rostralmost point of contribution of these turbinals to the cribriform plate. However, the transverse lamina does not contribute to the cribriform plate. Similarly, the maxillary recess extends caudally almost to the point of contribution of the cribriform plate. The rostral portion of the lamella of the ventralmost ectoturbinal is attached to the posterior transverse lamina.

The encranial surface of the cribriform plate of *Myrmecobius* is similar to the general

marsupial condition except that the vertical column of olfactory foramina bordering the crista galli is not continuous. There is a large, imperforate area between the cribroethmoidal foramen and the olfactory foramen immediately ventral. In addition, the cribroethmoidal foramen is laterally offset from the medial edge of the cribriform plate.

The rostralmost point of ossification of the nasal septum is rostral to the crowns of the upper canines.

Myrmecobius lacks a frontal sinus, but a maxillary recess that is medially bordered by the posterior transverse lamina is present.

TARSIPEDIDAE: I examined CT images of a skull of *Tarsipes rostratus*, the only extant member of this taxon (Wilson and Reeder, 2005). The morphology of the rostral maxilloturbinal is simple; the medial end of the lamella bifurcates only once. The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines.

Tarsipes lacks an ossified rostral nasoturbinal, and consequently endoturbinal I projects more rostrally in the nasal cavity than the nasoturbinal. The rostral portion of the caudal nasoturbinal is straight and oriented parallel to the portion of the maxilla forming the nasal cavity lateral wall and at an oblique angle to the ossified nasal septum. An ossified uncinat process of the nasoturbinal is absent. The caudalmost point of ventral attachment of the nasoturbinal is on the lateral wall of the nasal cavity at a spot that is rostral to the caudal terminus of the maxilloturbinal.

Tarsipes has the fewest number of turbinal elements of any marsupial with three endoturbinals and one ectoturbinal (figs. 18 and 21).

The caudal portion of endoturbinal I has three turbinal lobes, but lacks any turbinal folds (fig. 20). Similarly, the caudal portion of endoturbinal II lacks turbinal folds, but it is bilaminar in morphology, and closely resembles the morphology of endoturbinal III of those marsupials with five elements.

Morphologically and topologically, endoturbinal III of *Tarsipes* resembles endoturbinal V of those marsupials with five elements. The caudal portion of endoturbinal III, which is sequestered in the sphenoidal recess,

is bilaminar with only one branch ending in a scroll. The lamella of endoturbinal III is attached to the lateral wall of the nasal cavity at the rostralmost point of contribution of the turbinal to the cribriform plate. At this point, the turbinal folds of endoturbinal III are asymmetrical in size.

The lamella of the only ectoturbinal of *Tarsipes* does not contact the posterior transverse lamina.

The rostral portion of the posterior transverse lamina is oriented at a roughly 45° angle to the palate and caudally the lamina is nearly parallel to the palate. The vomer of *Tarsipes* lacks an ossified paraseptal shelf that normally would contribute to the posterior transverse lamina. Despite the lack of the paraseptal shelves, the caudal portion of the vomer still fuses with the ethmoid to form the posterior transverse lamina.

The encranial surface of the cribriform plate of *Tarsipes* is similar to the general marsupial condition except that the vertical column of olfactory foramina bordering the crista galli is not continuous. There is a large, imperforate area between the cribroethmoidal foramen and the olfactory foramen immediately ventrally. In addition, there is also an imperforate area between the cribroethmoidal foramen and the endocranial cavity roof. The cribroethmoidal foramen is laterally offset from the medial edge of the cribriform plate.

The rostralmost point of ossification of the nasal septum is caudal to the crowns of the upper canines. Two pairs of swell bodies are documented at the base of the rostral portion of the nasal septum of *Tarsipes* (Kratzing, 1982).

Tarsipes lacks a maxillary recess and a frontal sinus.

PETAURIDAE: I examined a specimen of *Petaurus breviceps* as a representative of this clade, which includes 11 extant species distributed in three genera (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines. The lamella of the maxilloturbinal is attached to the medial surface of the caudal nasoturbinal (C136–142).

The rostral nasoturbinal is absent as an ossified structure, and consequently endoturbinal I projects more rostrally in the skull

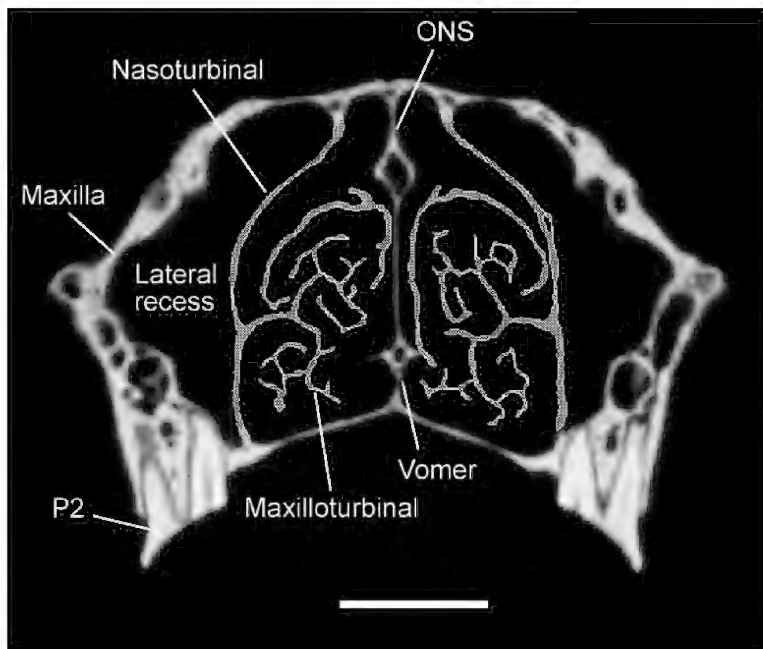


Fig. 33. Coronal CT image showing the contact between the maxilloturbinal and nasoturbinal (char. 4.1) in *Petauroides volans*, C385 (AMNH 150055). The plesiomorphic condition for marsupials is the lack of contact between these two elements (char. 4.0). Scale bar equals 5 mm. Abbreviations: ONS, ossified nasal septum; P2, second upper premolar.

than the nasoturbinal. The rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at nearly a right angle to each other. Caudal to this, the nasoturbinal has a laterally projecting branch that bifurcates into two turbinal lobes in *Petaurus* (C141–154), similar to the morphology seen in *Caenolestes*. The morphology of this projection resembles an ectoturbinal. Caudal to the division of the nasoturbinal around endoturbinal I, the caudodorsal portion of the caudal nasoturbinal is curled (C152–157). An ossified uncinuate process of the nasoturbinal is absent. The caudalmost point of ventral attachment of the nasoturbinal is on the lateral wall of the nasal cavity and rostral to the caudal terminus of the maxilloturbinal.

Petaurus has five endoturbinates and three ectoturbinates (table 4).

The lamella of endoturbinal V is attached to the floor of the sphenoidal recess at the rostralmost point of contribution of this turbinal to the cribriform plate. At this point, the turbinal folds of endoturbinal V are asymmetrical in size.

Ectoturbinal 3 (ventralmost ectoturbinal) of *Petaurus* has the simple morphology of a lamella that lacks bifurcations and ends in a slight bend. The lamella of this ectoturbinal does not contact the posterior transverse lamina. This ectoturbinal also does not contribute to the cribriform plate.

The rostral portion of the posterior transverse lamina is oriented at a roughly 45° angle to the palate and caudally the lamina is subparallel to the palate.

The encranial surface of the cribriform plate of *Petaurus* is similar to the general marsupial condition except that the vertical column of olfactory foramina bordering the crista galli is not continuous. There is a large, imperforate area between the cribroethmoidal foramen and the olfactory foramen immediately ventrally, and between the cribroethmoidal foramen and the endocranial cavity roof. In addition, the cribroethmoidal foramen is laterally offset from the medial edge of the cribriform plate. The cribroethmoidal foramen is not the largest of the foramina in the column.

The rostralmost point of ossification of the nasal septum is rostral to the crowns of the upper canines.

Petaurus lacks a maxillary recess and a frontal sinus.

PSEUDOCHEIRIDAE: I examined specimens of *Petauroides volans*, *Pseudocheirus occidentalis*, and *Pseudochirops cupreus* as representatives of Pseudocheiridae, which comprises 17 extant species distributed in six genera (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines in all three species. There is extensive contact between the maxilloturbinal and the nasoturbinal in *Petauroides* (fig. 33; C351–449). The lamella of the maxilloturbinal is attached to the medial surface of the caudal nasoturbinal along the majority of the caudal length of the maxilloturbinal. There is no contact between the maxilloturbinal and the nasoturbinal in the other two pseudocheirids. The caudalmost attachment point of the maxilloturbinal is on the floor of the nasal cavity in *Petauroides* and *Pseudocheirus*, whereas this attachment point is on the lateral wall of the nasal cavity in *Pseudochirops*.

Petauroides and *Pseudochirops* lack an ossified rostral nasoturbinal, but *Pseudocheirus* has a small, robust rostral nasoturbinal. However, in all three taxa endoturbinal I projects more rostrally in the nasal cavity than the nasoturbinal. The rostral portion of the caudal nasoturbinal is straight and oriented parallel to the portion of the maxilla forming the nasal cavity lateral wall and at an oblique angle to the ossified nasal septum in *Pseudochirops*. However, this portion of the nasoturbinal is kinked in the other two pseudocheirids. The rostral portion of the caudal nasoturbinal of *Petauroides* has at least three attachment points on the nasal cavity roof and lateral wall (C333–346 on right; C353–360 on left). Caudal to this, the rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at an obtuse angle in *Petauroides*. The rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at an acute angle in *Pseudocheirus*.

The caudal nasoturbinal is unbranched in *Pseudochirops*. Conversely, the caudal

nasoturbinal of *Petauroides* has a single laterally projecting turbinal branch (C444–470), and there is a long ventrolaterally projecting branch off the nasoturbinal in *Pseudocheirus* (C283–292). The caudal nasoturbinal of *Pseudocheirus* lacks pneumatic cavities, but there is a single pneumatic vacuity near the center of this element in *Petauroides* (C471–492) and in *Pseudochirops* (C412–460).

The caudodorsal portion of the caudal nasoturbinal, posterior to the division of the nasoturbinal around the lamella of endoturbinal I, is curled in *Petauroides* (C470–500), but it is unfolded in the other two pseudocheirids. An ossified uncinat process of the nasoturbinal is absent in all three taxa. The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the lacrimal canal and rostral to the caudal terminus of the maxilloturbinal in *Pseudocheirus*. In *Petauroides*, the caudalmost point of ventral attachment of the nasoturbinal is on the maxilloturbinal, a unique condition among marsupials (fig. 15). The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the infraorbital canal (V_2) and in the same coronal plane as the caudal terminus of the maxilloturbinal in *Pseudochirops*.

All three species of Pseudocheiridae examined here have the typical marsupial number of five endoturbinals and two ectoturbinals (table 4).

The rostral portion of endoturbinal I of *Pseudocheirus* and *Pseudochirops* contains small pneumatic vacuities, whereas this element in *Petauroides* lacks any cavities (fig. 19). The caudal portion of endoturbinal I of *Pseudochirops* lacks any turbinal folds. The caudal portion of endoturbinal III near its contribution to the cribriform plate only has one turbinal fold in *Pseudocheirus* and *Petauroides*. The rostral portion of endoturbinal IV is branched at its medial terminus in *Pseudocheirus* and *Petauroides* unlike the condition in *Pseudochirops*. The caudal portion of endoturbinal V, which is sequestered in the sphenoidal recess, is unbranched and ends in a turbinal fold in *Pseudocheirus*. In contrast, the caudal portion of endoturbinal V of *Pseudochirops* is bilaminar but contains no turbinal folds. The lamella of endoturbinal

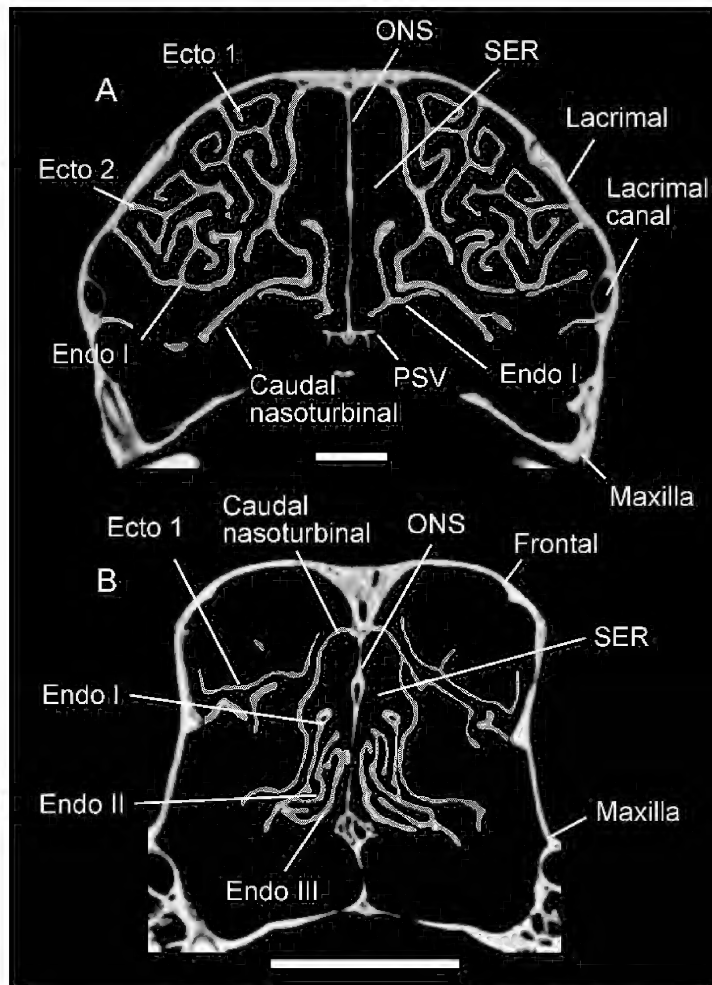


Fig. 34. Coronal CT images showing the presence or absence of a paraseptal shelf of the vomer (char 28). (A) shelf present (char. 28.0), *Caenolestes fuliginosus*, C389 (KU 124015), scale bar equals 1 mm; (B) shelf absent (char. 28.1), *Pseudocheirus occidentalis*, C273 (TMM M-847), scale bar equals 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; PSV, paraseptal shelf of vomer; SER, sphenethmoid recess.

V is attached to the floor of the sphenoidal recess at the rostralmost point of contribution of the turbinal to the cribriform plate in *Pseudocheirus*, *Pseudochirops*, and on the right side of the skull in *Petauroides*. At the point of contribution to the cribriform plate, the turbinal folds of endoturbinal V are asymmetrical in size in *Pseudochirops*.

The lamella of the ventralmost ectoturbinal of *Pseudocheirus* does not bifurcate. The lamella of the ventralmost ectoturbinal does

not contact the posterior transverse lamina in any of the pseudocheirids.

The posterior transverse lamina of the pseudocheirids is located caudal in the nasal cavity compared to other marsupials and endoturbinals I and II do not contribute to the lamina. In general, the transverse lamina is subparallel to the palate along its entire rostrocaudal length. The paraseptal shelf of the vomer is absent in *Pseudocheirus* (fig. 34). Despite the lack of the paraseptal shelves in *Pseudocheirus*, the caudal portion of the

vomer fuses with the ethmoid to form the posterior transverse lamina.

The encranial surface of the cribriform plate of pseudocheirids is similar to the general marsupial condition except that there is a large imperforate space above the vertical column of foramina that line the crista galli.

The rostralmost point of ossification of the nasal septum is caudal to the crowns of the upper canines in *Petauroides*, but rostral to the crowns in the other two pseudocheirids.

Pseudocheirus has a frontal sinus and a maxillary recess; the other two taxa lack both of these.

PHALANGERIDAE: I examined specimens of *Phalanger orientalis* and *Trichosurus vulpecula* as representatives of Phalangeridae, a clade which comprises 27 extant species distributed in six genera (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines in both phalangerid species.

Phalanger lacks an ossified rostral nasoturbinal, whereas *Trichosurus* has a small, robust rostral nasoturbinal. As a result, the nasoturbinal projects more rostrally than endoturbinal I in *Trichosurus*, but the opposite occurs in *Phalanger*. The rostrrodorsal and rostroventral portions of the caudal nasoturbinal are kinked at nearly a right angle in *Trichosurus*, but in *Phalanger* the kink forms an obtuse angle. The caudal nasoturbinal of *Phalanger* is unbranched, but in *Trichosurus* this element has two laterally projecting branches, one of which is directed dorsally and the other ventrally (C211). Caudal to the division of the nasoturbinal around endoturbinal I, the caudodorsal portion of the nasoturbinal is curled in both phalangerid species (fig. 13; C239–256 in *Phalanger*; C213–237 in *Trichosurus*). An ossified uncinat process is also present in both taxa. The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the infraorbital canal (V_2) in *Phalanger* and on the lateral wall of the nasal cavity in *Trichosurus* (fig. 15). The caudalmost extent of the ventral attachment of the nasoturbinal is at the same coronal level as the caudal terminus of the maxilloturbinal in *Trichosurus* but caudal to the maxilloturbinal in *Phalanger*.

Both *Phalanger* and *Trichosurus* have five endoturbinals and three ectoturbinals (table 4).

The caudal portion of endoturbinal I of *Trichosurus* has two turbinal folds, whereas there is the usual single fold on this element in *Phalanger*. The rostral portion of endoturbinal IV is unbranched at its medial terminus in *Trichosurus*, but has a terminal bifurcation in *Phalanger*. The caudal portion of endoturbinal V, which is sequestered in the sphenoidal recess, has only one turbinal fold in *Phalanger*, unlike the typical marsupial condition of two folds as present in *Trichosurus*. The lamella of endoturbinal V is attached to the lateral wall of the sphenoidal recess in *Phalanger*, but is attached to the floor of the recess in *Trichosurus*. The turbinal folds of endoturbinal V of *Trichosurus* are asymmetrical in size at the rostralmost point of contribution of this element to the cribriform plate.

The rostral lamella of the ventralmost ectoturbinal (ectoturbinal 3) of *Trichosurus* is attached to the posterior transverse lamina, but this does not occur in *Phalanger*.

The posterior transverse lamina is oriented nearly parallel to the nasal septum along most of its rostrocaudal length in both phalangerid species.

The encranial surface of the cribriform plate of the two phalangerids is similar to the general marsupial condition except that there is a large imperforate space above the vertical column of foramina that line the crista galli. The cribroethmoidal foramen of *Phalanger* is about the same size as the olfactory foramina that lie below it.

The rostralmost point of ossification of the nasal septum is in the same coronal plane as the crowns of the upper canines in *Trichosurus*, but caudal to the crowns of the canines in *Phalanger* (fig. 29).

Both phalangerid taxa have a maxillary recess with a caudomedial wall constructed exclusively from the posterior transverse lamina. *Phalanger* has a small frontal sinus (fig. 25), but *Trichosurus* lacks this sinus.

POTOROIDAE: I examined a specimen of *Potorous tridactylus* as a representative of this clade, which includes 10 extant species distributed in four genera (Wilson and Reeder, 2005). The rostralmost attachment

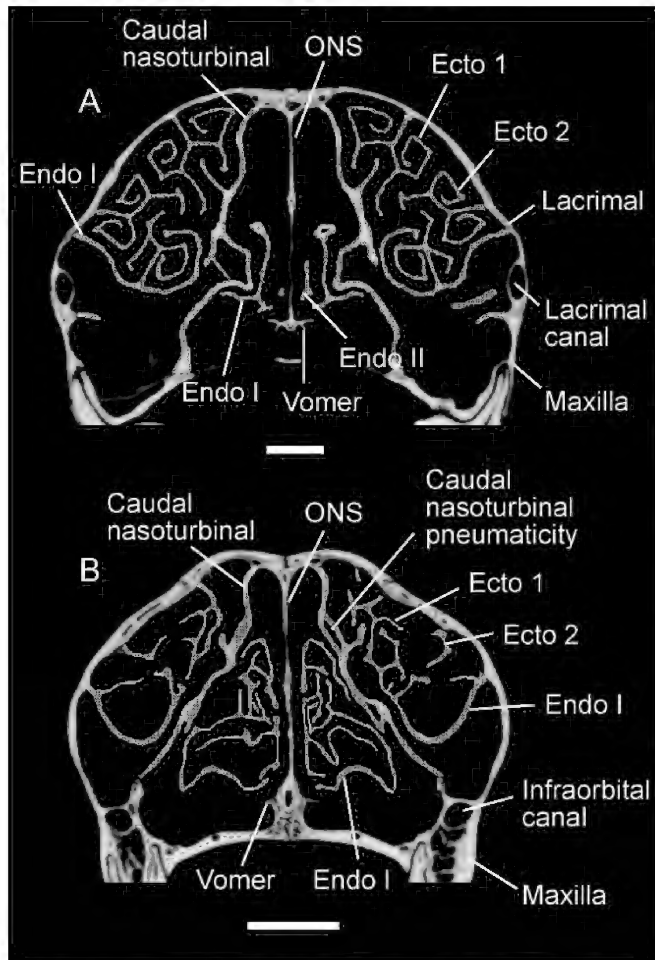


Fig. 35. Coronal CT images showing the presence or absence of pneumaticity in the caudal nasoturbinal (char. 8). (A) pneumaticity is absent (char. 8.0), *Caenolestes fuliginosus*, C400 (KU 124015), scale bar equals 1 mm; (B) pneumaticity is present (char. 8.1), *Potorous tridactylus*, C386 (AMNH 65337), scale bar equals 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum.

point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines.

Potorous has an ossified rostral nasoturbinal with a slender ventromedially directed morphology. The rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at an obtuse angle. The caudal nasoturbinal has multiple pneumatic vacuities near the center of the element (fig. 35; C382–405). The caudodorsal portion of the nasoturbinal (caudal to the division of the nasoturbinal around endoturbinal I) is curled (C399–454) and an ossified uncinate process is present. The caudalmost point of ventral attachment of the nasoturbinal is on the

medial wall of the lacrimal canal and posterior to the caudal terminus of the maxilloturbinal.

Potorous has five endoturbinals and four ectoturbinals (fig. 21; table 4).

The endo- and ectoturbinals of *Potorous* are complexly branching and densely packed creating a tight mazelike pattern (fig. 6), especially around the ossified nasal septum. Endoturbinal I of *Potorous* has three turbinal folds and multiple turbinal lobes in its most complex coronal section (e.g., C459–471). Endoturbinal II has three turbinal lobes just anterior to its rostralmost point of contribution to the cribriform plate (e.g., C483–496). The rostral portion of endoturbinal III is

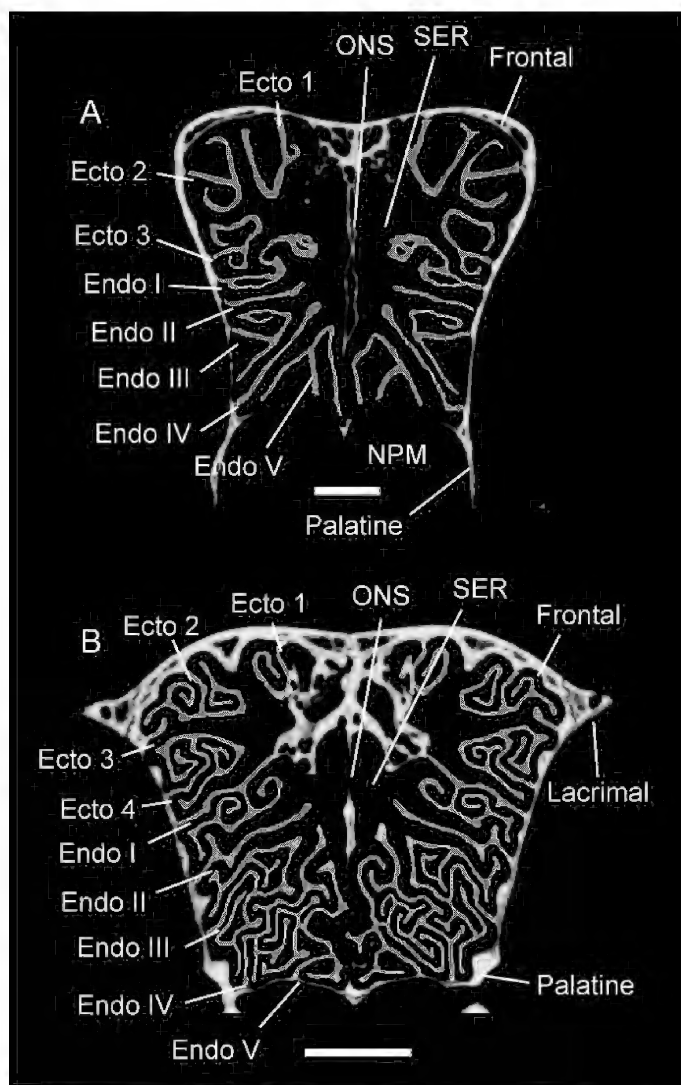


Fig. 36. Coronal CT images showing the morphology of the ventral portion of ossified nasal septum (char. 30). (A) ventral portion is straight or only with slight bends or convolutions (char. 30.0), *Wallabia bicolor*, C430 (TMM M-4169); (B) ventral portion is very convoluted (char. 30.1), *Potorous tridactylus*, C495 (AMNH 65337). Both scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; NPM, nasopharyngeal meatus; ONS, ossified nasal septum; SER, sphenethmoid recess.

elongated and contains multiple terminal branches that are convoluted. However, endoturbinal III is bilaminar with each branch ending in a scroll near its point of contribution to the cribriform plate. Endoturbinal IV is branched at its medial terminus along its entire length. The lamella of endoturbinal V is attached to the lateral wall of the sphenoidal recess at the rostralmost point of contribution of this turbinal to the cribriform plate.

The two dorsalmost and the ventralmost ectoturbinals are bilaminar with each branch ending in a convoluted scroll. Ectoturbinal 3 is considerably smaller than the other ectoturbinals and barely contributes to the cribriform plate. Ectoturbinal 3 also differs morphologically; although this element bifurcates, it contains no scrolls. The rostral portion of the lamella of ectoturbinal 4 is attached to the posterior transverse lamina.

The rostral portion of the posterior transverse lamina is oriented at an approximately 45° angle to the palate, but caudally the lamina is oriented nearly parallel to the nasal septum.

The encranial surface of the cribriform plate of *Potorous* is similar to the general marsupial condition except that the vertical column of olfactory foramina bordering the medial edge of the plate is not continuous. The imperforate areas between the top three olfactory foramina are larger than the areas between the more ventral foramina. In addition, the dorsalmost olfactory foramen is slightly laterally offset from the medial edge of the cribriform plate. The cribroethmoidal foramen, the largest of the foramen in the column, lies immediately below the dorsalmost olfactory foramen.

The rostralmost point of ossification of the nasal septum is rostral to the crowns of the upper canines. The ventral portion of the nasal septum is convoluted for the caudal one-fourth of the ossified septum (fig. 36; C425–543). A crista galli is absent.

The maxillary recess is present but a frontal sinus is absent.

HYPSPRYMNODONTIDAE: I examined CT images of a skull of *Hypsiprymnodon moschatus*, the only extant member of this taxon (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity rostral to the roots of the upper canines.

Hypsiprymnodon has a small, robust, ventromedially inflected rostral nasoturbinal. The rostral portion of the caudal nasoturbinal of *Hypsiprymnodon* resembles that of *Dasyurus* and *Echymipera*. The dorsal portion of the nasoturbinal is in the shape of a boomerang with the ends oriented dorsally and laterally and the ventral portion is curved with the convex surface facing the lateral recess (C240–255). The caudodorsal portion of the caudal nasoturbinal is curled (C318–356), posterior to the division of the nasoturbinal around endoturbinal I. An ossified uncinate process is also present. The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the lacrimal canal, and the caudalmost extent of the attachment is rostral to the caudal terminus of the maxilloturbinal.

Hypsiprymnodon has five endoturbinals and three ectoturbinals (table 4).

The caudal portion of endoturbinal I of *Hypsiprymnodon* has two turbinal folds and three turbinal lobes. The caudal part of the lamella of endoturbinal V is attached to the floor of the nasal cavity at the rostralmost point of contribution of the turbinal to the cribriform plate.

All three of the ectoturbinals of *Hypsiprymnodon* have bilaminar rostral portions with each branch terminating in a scroll. However, ectoturbinal 3 consists of a single scroll at the point of contribution of this turbinal to the cribriform plate. The rostral portion of the lamella of ectoturbinal 3 is attached to the posterior transverse lamina.

The rostral portion of the posterior transverse lamina is oriented at a 45° angle to the palate and caudally the lamina is oriented nearly parallel to the nasal septum.

The encranial surface of the cribriform plate of *Hypsiprymnodon* is similar to the general marsupial condition except that the vertical column of olfactory foramina bordering the medial edge of the plate is not continuous. There is a large, imperforate area between the cribroethmoidal foramen and the olfactory foramen immediately ventrally. In addition, the cribroethmoidal foramen is laterally offset from the medial edge of the cribriform plate.

The rostralmost point of ossification of the nasal septum is rostral to the crowns of the upper canines. A crista galli is present.

Hypsiprymnodon has a maxillary recess but lacks a frontal sinus.

PHASCOLARCTIDAE: I examined CT images of a skull of *Phascolarctos cinereus*, the only extant member of this taxon (Wilson and Reeder, 2005). The rostral maxilloturbinal consists of an unbranched lamella that terminates in a scroll (figs. 28 and 37). The rostralmost extent of the maxilloturbinal is just anterior to the roots of the upper canines. The caudalmost fifth of the maxilloturbinal of *Phascolarctos* is unique in that it is unattached to the nasal cavity walls or floor and becomes an enclosed tube that tapers into a cone (figs. 37 and 38). This unique morphology was noted by Paulli (1900a) who described the caudal portion of the maxilloturbinal as resulting from pneumatization of the element.

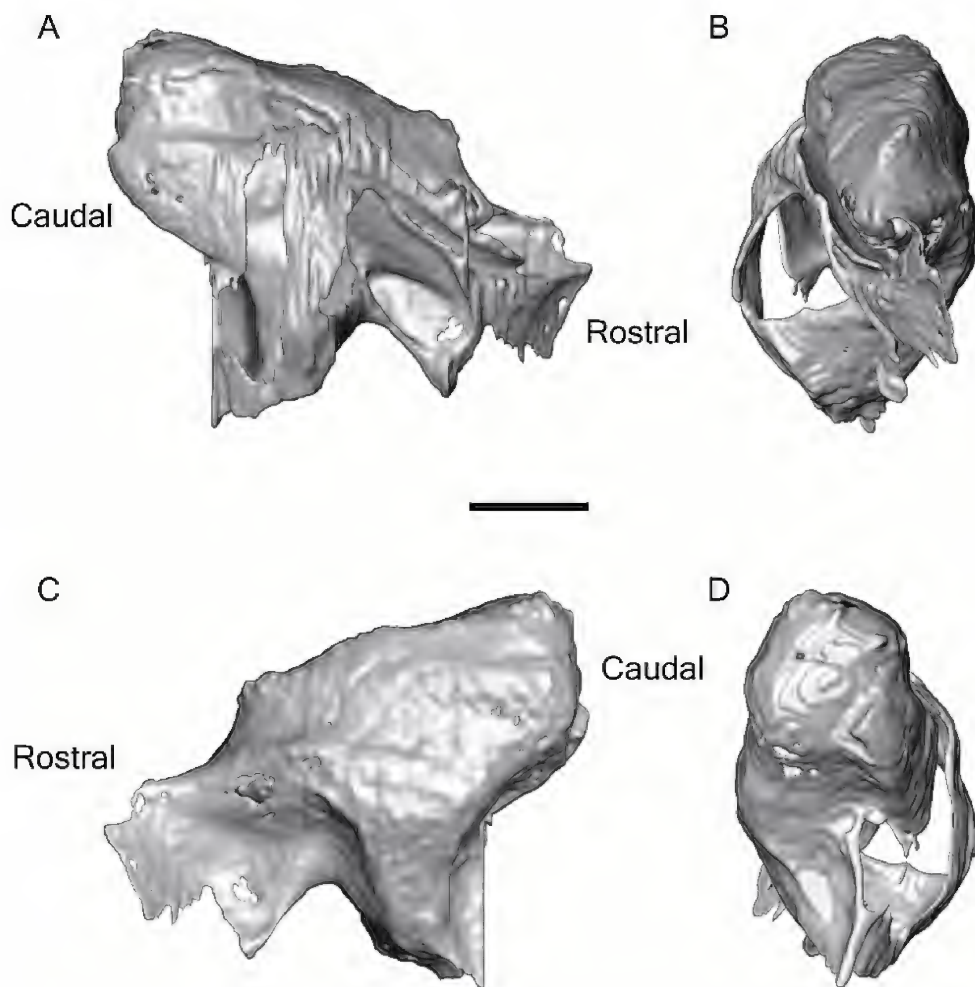


Fig. 37. Digital rendering of the isolated right maxilloturbinal from *Phascolarctos cinereus* (TMM M-2946) shown in (A) lateral, (B) rostral, (C) medial, and (D) caudal views. Labels indicate caudal and rostral ends of the maxilloturbinal for the lateral and medial views. Scale bar equals 1 cm.

Kratzing (1984: 64) also notes that the ventral concha (maxilloturbinal) of the koala is “recurved to form a bulb.” This maxilloturbinal morphology is also present in *Vombatus*. The caudalmost attachment of the maxilloturbinal is to the lateral wall of the nasal cavity rather than the floor of the cavity as in most marsupials.

The rostral nasoturbinal is a slender, ventrally directed structure that projects nearly as far anterior as the maxilloturbinal and extends posteriorly for about two-thirds the length of the entire nasoturbinal. The rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at nearly

a right angle. Caudally, the nasoturbinal does not divide around the root of endoturbinal I as in all other marsupials. The caudalmost point of ventral attachment of the nasoturbinal is on the lateral wall of the nasal cavity and is located posterior to the caudal terminus of the maxilloturbinal.

I report that *Phascolarctos* has five endoturbinals and one ectoturbinal (table 4), but others reported fewer elements (Paulli, 1900a; Kratzing, 1984). According to the description by Paulli (1900a) and applying my nomenclature, the koala has five endoturbinals and no ectoturbinals. Ectoturbinal 1 of the koala was considered to be a caudal

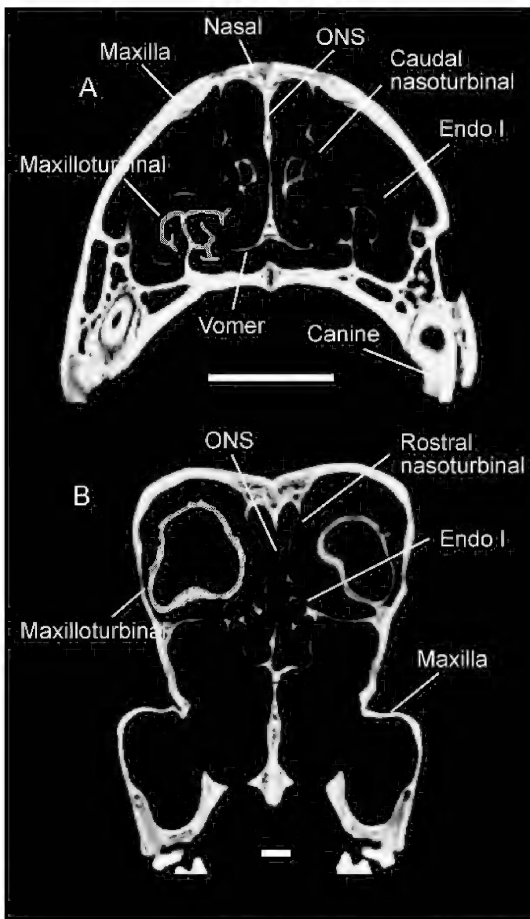


Fig. 38. Coronal CT images showing the morphology of the caudalmost portion of the maxilloturbinal in marsupials (char. 2). (A) caudal maxilloturbinal is simple in morphology and is attached to the nasal cavity wall or floor (char. 2.0), *Isoodon macrourus*, C314 (TMM M-6922); (B) caudalmost portion of maxilloturbinal becomes an enclosed tube that tapers into a cone that is unattached to the nasal cavity (char. 2.1), *Phascolarctos cinereus*, C251 (TMM M-2946). Both scale bars equal 5 mm. Abbreviations: Endo, endoturbinal; ONS, ossified nasal septum.

portion of the nasoturbinal by Paulli (1900a), but examination of the CT imagery of a koala skull indicates that clearly this is not the case, at least not for the specimen examined here. Kratzing (1984) reported four endoturbinals and one ectoturbinal for *Phascolarctos*.

Phascolarctos lacks a rostral projection of endoturbinal I that overlies the maxilloturbinal (fig. 39). Instead, the maxilloturbinal ac-

tually overlies endoturbinal I which is reversed from the typical marsupial condition. The morphology of endoturbinal I of the koala is simple. Rostrally, the lamella of endoturbinal I has a terminal bifurcation, but caudally the element lacks branches (fig. 39). Endoturbinal I has no turbinal folds anywhere along its length. Endoturbinals II and IV do not contribute to the cribriform plate. The caudal portion of endoturbinal III that is near its contribution to the cribriform plate is simple in morphology and lacks any branches or turbinal folds. The endoturbinal V of *Phascolarctos*, which has a single turbinal fold, is never sequestered in a sphenoidal recess unlike the condition in other marsupials. Instead, the nasal cavity comes to an abrupt termination, rather than tapering off into a sphenoidal recess as in other marsupials.

Phascolarctos only has one ectoturbinal, which is tubelike in shape caudally, similar to the maxilloturbinal (fig. 40; C260–284). The ectoturbinal does not contribute to the cribriform plate.

The posterior transverse lamina is roughly oriented at a 45° angle to the palate along most of its length. The paraseptal shelves of the vomer are absent in the koala. Despite the lack of the paraseptal shelves, the caudal portion of the vomer fuses with the ethmoid to form the posterior transverse lamina.

The encranial surface of the cribriform plate of *Phascolarctos* is similar to the general marsupial condition except that there is a large imperforate space above the vertical column of foramina that line the crista galli. The cribroethmoidal foramen is the largest and dorsalmost of the foramen in the column.

The rostralmost point of ossification of the nasal septum is caudal to the crowns of the upper canines. Prominent lateral expanded bulges are absent within the shaft of the ossified nasal septum. In addition, *Phascolarctos* lacks swell bodies at the base of the nasal septum (Kratzing, 1984).

Phascolarctos does not have a maxillary recess, but the frontal sinus is well developed.

VOMBATIDAE: I examined CT images of a skull of *Vombatus ursinus* as a representative of this clade, which includes three extant species distributed in two genera (Wilson and Reeder, 2005). The morphology of the rostral

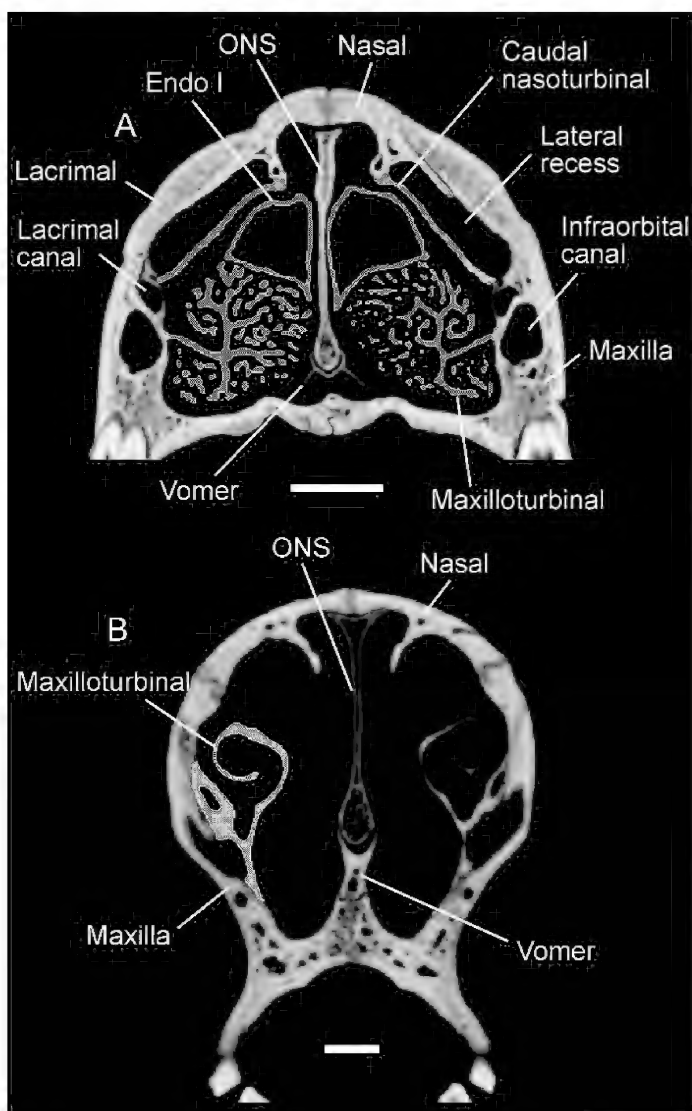


Fig. 39. Coronal CT images showing the presence or absence of the rostral portion of endoturbinial I (char. 16). (A) rostral portion present (char. 16.0), *Didelphis virginiana*, C270 (TMM M-2517); (B) rostral portion absent (char. 16.1), *Phascolarctos cinereus*, C129 (TMM M-2946). Both scale bars equal 5 mm. Abbreviations: Endo, endoturbinial; ONS, ossified nasal septum.

maxilloturbinal is an unbranched lamella that is curled at its medial end (e.g., C081–114). The caudalmost fifth of the maxilloturbinal is unattached to the nasal cavity walls or floor and becomes an enclosed tube that tapers into a cone, similar to the condition in *Phascolarctos*. The rostralmost attachment point of the maxilloturbinal of *Vombatus* is above the crypt holding the extensive root of the upper incisor.

Vombatus has a well-developed ossified rostral nasoturbinal that extends posteriorly for about two-thirds the length of the entire nasoturbinal. The rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at nearly a right angle. The caudal nasoturbinal has several pneumatic vacuities near the center of the element (C166–188). An ossified uncinat process is present. The caudalmost point of ventral attachment of

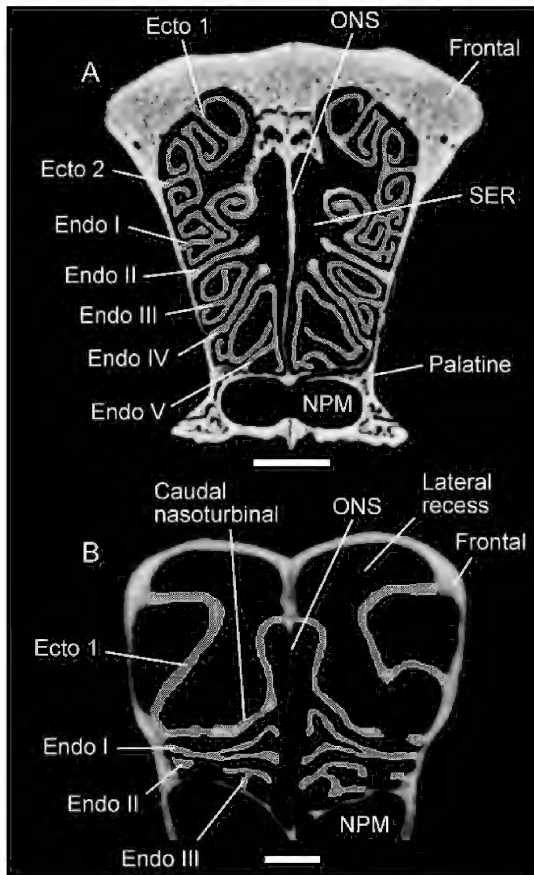


Fig. 40. Coronal CT images showing the tube like morphology of the ectoturbinals (char. 21). (A) tube like morphology absent (char. 21.0), *Didelphis virginiana*, C464 (TMM M-2517); (B) ectoturbinals are tube like in shape (char. 21.1), *Phascolarctos cinereus*, C273 (TMM M-2946). Both scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; NPM, nasopharyngeal meatus; ONS, ossified nasal septum; SER, sphenethmoid recess.

the nasoturbinal is on the lateral wall of the nasal cavity and posterior to the caudal terminus of the maxilloturbinal.

Vombatus has seven endoturbinals and two ectoturbinals (fig. 18; table 4).

The endo- and ectoturbinals of *Vombatus* are convoluted and are densely packed creating a tight mazelike pattern, especially around the ossified nasal septum (fig. 18). *Vombatus*, like *Phascolarctos*, lacks a rostral projection of endoturbinal I that overlies the maxilloturbinal. Instead, the maxilloturbinal actually overlies endoturbinal I, which is reversed

from the typical marsupial condition. The caudal portion of endoturbinal I does have branches off the lamella, but there are no turbinal folds. Endoturbinal II is a simple element that is curved at its terminus and endoturbinal III of *Vombatus* has a morphology that closely resembles that of endoturbinal II of marsupials with only five elements. The caudal portion of endoturbinal IV, near its contribution to the cribriform plate, only has one turbinal fold. The rostral portion of endoturbinal V is branched at its medial terminus, whereas the caudal portion of this endoturbinal, near its contribution to the cribriform plate, is unbranched. Endoturbinal VI is bifurcated at its medial terminus and these branches end in slight turbinal folds. The caudal portion of endoturbinal VII, which is sequestered in the sphenoidal recess, is unilaminar and lacks scrolls.

The posterior transverse lamina is roughly oriented at a 45° angle to the palate rostrally, but caudally it is subparallel to the palate. The paraseptal shelves of the vomer are absent in *Vombatus*. Despite the lack of the paraseptal shelves, the caudal portion of the vomer still fuses with the ethmoid to form the posterior transverse lamina.

The cribriform plate of *Vombatus* does not differ significantly from the generalized marsupial condition.

The rostralmost point of ossification of the nasal septum is around the rostralmost extension of the maxilloturbinal. The ossified nasal septum is a fairly straight, vertically oriented element along most of its length, except for the caudal one-fourth in which the ventral portion of the nasal septum is convoluted (fig. 18; C193–230). Prominent lateral expanded bulges are not found within the shaft of the ossified nasal septum. A crista galli is present.

Vombatus does not have a maxillary recess, but the frontal sinus is well developed.

MACROPODIDAE: I examined *Dendrolagus lumholtzi* and *Wallabia bicolor* as representatives of this clade, which includes 65 extant species distributed in 11 genera (Wilson and Reeder, 2005). The rostralmost attachment point of the maxilloturbinal is on the lateral wall of the nasal cavity and rostral to the roots of the third upper incisors in *Dendrolagus*, but this attachment is caudal to the roots in *Wallabia*. The caudalmost attachment

point of the maxilloturbinal is on the floor of the nasal cavity in *Dendrolagus*, but on the lateral wall of the cavity in *Wallabia*.

Both macropodids have a short, robust, ossified rostral nasoturbinal. The rostral portion of the caudal nasoturbinal of *Wallabia* is straight and oriented parallel to the portion of the maxilla forming the nasal cavity lateral wall and at an oblique angle to the ossified nasal septum. However, the rostradorsal and rostroventral portions of the caudal nasoturbinal are kinked at nearly a right angle in *Dendrolagus*. Caudally, an ossified uncinat process is present in both taxa. The caudalmost point of ventral attachment of the nasoturbinal is on the medial wall of the lacrimal canal in both macropodids. The caudalmost extent of the attachment of the nasoturbinal is at the same coronal level as the caudal terminus of the maxilloturbinal in *Dendrolagus*, but posterior to the maxilloturbinal in *Wallabia*.

The macropodids examined in this study have four or five endoturbinals and two or three ectoturbinals (table 4). *Dendrolagus* has four endoturbinals (fig. 18), whereas *Wallabia* has five endoturbinals. A figure of the nasal cavity of *Petrogale penicillata* by Paulli (1900a) indicates that this species also has all five endoturbinals.

The rostral portion of endoturbinal II of *Dendrolagus* is unilaminar, but ends in a turbinal fold. Likewise, the caudal portion of endoturbinal II is unilaminar, but the turbinal fold is absent. Endoturbinal IV, which has one turbinal fold, is sequestered in the lateral recess and its lamella attaches to the floor of the nasal cavity. At the point of contribution to the cribriform plate, the turbinal folds of endoturbinal IV are asymmetrical in size. The morphology and topology of endoturbinal IV of *Dendrolagus* most closely resembles that of endoturbinal V of a marsupial with five elements.

Endoturbinals I, II, and IV of *Wallabia* are unremarkable compared to the generalized marsupial condition. Endoturbinal III is bilaminar and caudally it ends with two turbinal folds. Endoturbinal V of *Wallabia* has two folds, and its lamella is attached to the lateral wall of the nasal cavity of the sphenoidal recess. At the point of contribu-

tion to the cribriform plate, the turbinal folds of endoturbinal V are asymmetrical in size.

Wallabia has three ectoturbinals (fig. 21), as does *Petrogale penicillata* (Paulli, 1900a), whereas *Dendrolagus* has the usual marsupial number of two. The rostral portions of all three ectoturbinals in *Wallabia* are bilaminar, but the dorsalmost ectoturbinal is unilaminar caudally. Both ectoturbinals of *Dendrolagus* are unilaminar along their entire length (fig. 41). The rostral lamella of the ventralmost ectoturbinal is attached to the posterior transverse lamina in both taxa.

The rostral portion of the posterior transverse lamina is oriented at a 45° angle to the palate, but caudally the lamina is nearly parallel to the nasal septum in *Wallabia*. The transverse lamina is oriented subparallel to the palate along its entire length in *Dendrolagus*.

The cribriform plate of *Wallabia* does not differ significantly from that of the generalized marsupial condition. In *Dendrolagus*, there is an imperforate space above the row of olfactory foramina lining the medial border of each ethmoid, and the cribroethmoidal foramen is more laterally placed than in the generalized marsupial condition.

The rostralmost point of ossification of the nasal septum is caudal to the crowns of the upper third incisors. Prominent lateral expanded bulges are present within the shaft of the ossified nasal septum in *Dendrolagus* but absent in *Wallabia* (fig. 24). Both macropodid species lack a crista galli (fig. 23).

A maxillary recess is absent in *Dendrolagus*, but present in *Wallabia*. *Dendrolagus* has a large frontal sinus (fig. 25), but *Wallabia* lacks this sinus.

Intraspecific Variation

ONTOGENETIC VARIATION: Examination of ontogenetic variation is based on the growth series of 18 specimens of *Monodelphis domestica*. There is no variation in the number of bony turbinal elements in this growth series, that is, the same number of bony turbinal elements present in adult *M. domestica* is visible by postnatal day 27 (PND-27). The cartilaginous precursors of these bony turbinal elements are all present in

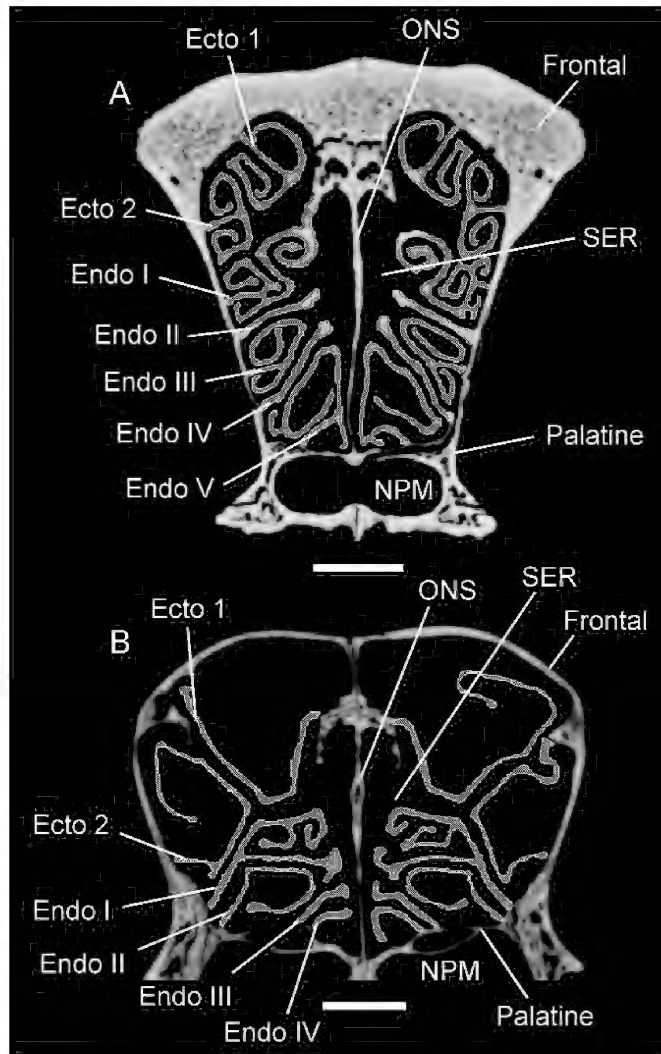


Fig. 41. Coronal CT images showing differences in the morphology of the ventralmost ectoturbinal (char. 20). (A) ventralmost ectoturbinal bifurcates (char. 20.0), *Didelphis virginiana*, C464 (TMM M-2517); (B) ventralmost ectoturbinal does not bifurcate (char. 20.1), *Dendrolagus lumholtzi*, C280 (AMNH 65254). Both scale bars equal 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; NPM, nasopharyngeal meatus; ONS, ossified nasal septum; SER, sphenethmoid recess.

the chondrocranium by PND-14 (Freyer, 1999).

However, ontogenetic variation is evident in the morphology of the turbinals. The maxilloturbinal in PND-27 specimens of *M. domestica* only has a single, simple scroll in contrast to the more complex morphology present in adults. The adult morphology of the maxilloturbinal is characterized by a scroll with at least two full turns (720°)

rostrally as well as a more complicated structure caudally, including several additional branches. The adult morphological condition of the maxilloturbinal is visible by PND-75.

There is contact between the maxilloturbinal and the caudal nasoturbinal in one of the three PND-27 specimens (TMM M-7595), and both PND-48 individuals. The lamella of the maxilloturbinal is split into two roots that

attach to the wall of the nasal cavity and form the rostromedial wall of the lacrimal canal. The dorsalmost of these two roots is attached to the caudal nasoturbinal in the PND-27 and PND-48 individuals.

The turbinal fold on endoturbinal I in the PND-27 opossums (e.g., TMM M-7595) is only a slight curl and not a true scroll as is present in the older individuals. Endoturbinal III is unilaminar and lacks turbinal folds near the point of contribution to the cribriform plate in a PND-27 individual (TMM M-7595). This turbinal also lacks folds in both PND-48 and the PND-56 specimens.

Endoturbinal V has no turbinal folds in the only PND-27 individual in which this character is assessable. In all the older opossums, endoturbinal V has two turbinal folds.

The rostral extent of ossification of the nasal septum is caudal to the crowns of the upper canines in all subadult opossums.

INDIVIDUAL VARIATION: Variation in the morphology of the ethmoid between individuals of the same age is also evident based on this sample of *Monodelphis domestica*.

The caudodorsal portion of the caudal nasoturbinal (caudal to the division around endoturbinal I) is curved (C322–350; character state 10.1) in one individual of *M. domestica*, a two-month-old individual (TMM M-9040). None of the other specimens showed any type of folding in this portion of the caudal nasoturbinal.

The caudalmost extent of the ventral attachment of the nasoturbinal is posterior to the caudal terminus of the maxilloturbinal (char. state 13.2) in the majority of the individuals (10 of 18) of *M. domestica* that were examined. However, in the remaining individuals the caudalmost extent of the attachment of the nasoturbinal occurred at the same coronal level as the caudal terminus of the maxilloturbinal (char. state 13.1). The individuals showing this character state includes one PND-27 specimen (TMM M-7595), both PND-48 specimens, the PND-56 specimen, the PND-57 specimen, the PND-76 specimen, one PND-90 specimen (TMM M-8268), and an adult specimen (TMM M-8271).

Endoturbinal III has a clear contribution to the cribriform plate in most of the

specimens of *M. domestica* I examined and marsupials in general. However, in two adult opossums (TMM M-9038 and TMM M-8273), one PND-48 individual (TMM M-8269), and the PND-75 opossum endoturbinal III is diminutive and has only a slight contribution to the cribriform plate.

The rostral portion of endoturbinal IV is unbranched in the majority of the *Monodelphis domestica* examined but does show branching in three adults (TMM M-7599, TMM M-8271, and TMM M-8273), and two two-month-old individuals (TMM M-9041 and TMM M-9039). The caudal portion of endoturbinal IV is unbranched in all the specimens except for one adult (TMM M-7599).

The lamella of endoturbinal V is typically attached to the nasal cavity wall at its rostralmost contribution to the cribriform plate. However, in both of the specimens of PND-27 and PND-48 individuals in which this character is assessable, the PND-56 specimen, and the PND-76 individual, the lamella attaches to the nasal cavity floor at its rostralmost contribution to the cribriform plate. The lamella of endoturbinal V of the PND-75 individual attaches to the nasal cavity wall at its rostralmost contribution to the cribriform plate.

The rostral extent of ossification of the nasal septum is rostral to the crowns of the upper canines in two of the adult opossums, but is even with the crowns in the other two adults. The presence of a distinctive crista galli is variable in *Monodelphis domestica*, being present in all the two-month-old specimens, the PND-75 individual, and one adult (TMM M-8271).

ASYMMETRIES WITHIN THE SAME INDIVIDUAL: There are some asymmetries between the right and left ethmoid elements within the same individual in a few of the marsupial taxa in my sample.

The caudalmost extent of the ventral attachment of the nasoturbinal is posterior to the caudal terminus of the maxilloturbinal on the right side of the skull of *Echymipera*, whereas the attachment is rostral to the maxilloturbinal on the left side.

The rostral portion of the caudal nasoturbinal of *Petauroides* has three attachment points on the nasal cavity roof and lateral

TABLE 6
Surface areas of turbinal elements of *Didelphis virginiana* (TMM M-2517) acquired using Amira

Element	Surface area (mm ²)
ossified nasal septum	1538.70
left maxilloturbinal	2431.90
right maxilloturbinal	2588.80
left nasoturbinal	444.20
right nasoturbinal	416.30
left ectoturbinal 1	1122.30
right ectoturbinal 1	1053.50
left ectoturbinal 2	549.40
right ectoturbinal 2	561.50
left endoturbinal I	2109.40
right endoturbinal I	2046.50
left endoturbinal II	397.40
right endoturbinal II	386.80
left endoturbinal III	430.80
right endoturbinal III	438.00
left endoturbinal IV	385.20
right endoturbinal IV	394.90
left endoturbinal V	781.40
right endoturbinal V	747.70
left posterior transverse lamina	411.80
right posterior transverse lamina	447.10

wall on the right side of the skull (C333–346), and four attachment points on the left side (C353–360).

Endoturbinal II branches off the turbinal lamella of endoturbinal I on the right side of this skull of *Trichosurus*, whereas on the left side the lamella of endoturbinal II is attached to the posterior transverse lamina (fig. 15).

Endoturbinal V of *Phascolarctos* bifurcates on the left side of the skull but not on the right side. In addition, the lamella of the right endoturbinal V is attached to the lateral wall of the nasal cavity at the point of contribution to the cribriform plate, whereas on the left side this element is attached to the floor of the cavity in *Phascolarctos* and one PND-90 specimen of *Monodelphis* (TMM M-7545).

Conversely, the lamella of endoturbinal V is attached to the floor of the sphenoidal recess at the rostralmost point of contribution of the turbinal to the cribriform plate on the right side of the skull, but on the left it is attached to wall of the recess in *Petauroides*. Likewise, endoturbinal VII in *Vombatus* is attached to the nasal cavity floor on the right side of the skull in the sphenoidal recess, but it is attached to the lateral wall of the recess on the left.

There is variation in the number of ectoturbinals in the skull of *Notoryctes*; on the right side of the skull there are three ectoturbinals, whereas the left side has only two. Ectoturbinal 3 (on the right) has a different morphology than either ectoturbinal 1 or 2. The ventralmost ectoturbinal (ectoturbinal 3) on the right side of the skull is unilaminar where it contacts the cribriform plate, whereas on the left side the ventralmost element (ectoturbinal 2) bifurcates.

Quantitative Data

The surfaces areas (SAs) of the turbinals, ossified nasal septum, and posterior transverse laminae were measured for *Didelphis virginiana* using Amira and are reported in table 6. Endoturbinal I has the greatest SA of the endoturbinals in *Didelphis*, similar to the condition in *Monodelphis domestica* (table 6; Rowe et al., 2005). However, unlike *Monodelphis*, the maxilloturbinal of *Didelphis* has the greatest SA of all of the turbinal elements. Even so, I estimate that the turbinals provide more SA for olfactory epithelium than respiratory epithelium by a significant margin in *Didelphis* as well as *Monodelphis* (table 6; Rowe et al., 2005). The total SA (respiratory and olfactory) provided by the ethmoid of *Didelphis* is more than an order of magnitude larger than for *Monodelphis* (~9055 mm² for the right side of *Didelphis* [table 6] versus ~594 mm² for the same side in *Monodelphis* [Rowe et al., 2005]). Considering that the skull length of the specimen of *Didelphis* is approximately three times the length of the skull of *Monodelphis*, the total surface area provided by the turbinals of *Didelphis* is significantly larger than would be expected if the difference in surface areas between the two species were a function of simple size scaling.

DISCUSSION

Character Distributions

I scored a matrix of 35 osteological characters (appendices II and III) based on observations of the nasal cavity on my sample of marsupials and five outgroups (table 1). Three of the 35 characters are punitively diagnostic for previously recognized marsupial clades and an additional

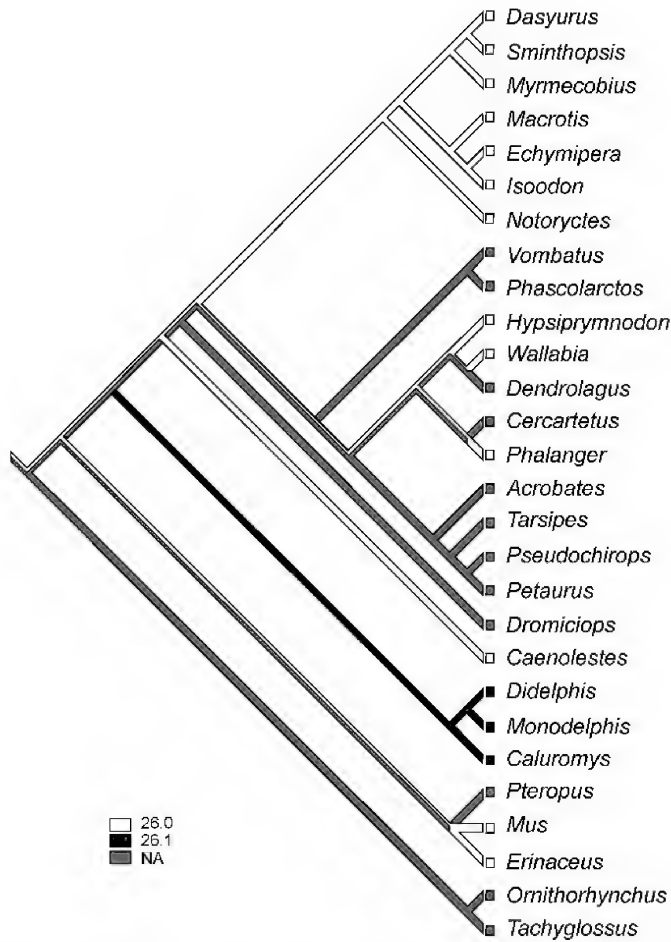


Fig. 42. Character 26 (morphology of the maxillary recess) optimized on the Meredith et al. (2009) topology. For character state 26.0, the caudal portion of recess is medially enclosed by the posterior transverse lamina. For character state 26.1, the uncinat process of the caudal nasoturbinat also contributes to the medial wall of the recess. States for this character are illustrated in figure 27. Abbreviation: NA, not applicable.

character is an equivocal synapomorphy for Marsupialia based on examination of these characters on the topologies of Meredith et al. (2009; fig. 1) and Sánchez-Villagra et al. (2007; fig. 2). I found one character that diagnoses Didelphidae and two characters that diagnose Vombatiformes (Vombatidae and Phascolarctidae).

The medial wall of the maxillary recess of didelphids is constructed from the uncinat process of the nasoturbinat and the posterior transverse lamina (character 26.1; fig. 42). This is contra the condition in other marsupials and the outgroups, in which the posterior transverse lamina is the sole con-

tributor to the medial wall of the maxillary recess (character 26.0; fig. 42).

The caudalmost portion of the maxilloturbinat becomes an enclosed tube that tapers into a cone that is unattached to the nasal cavity in the Vombatiformes (character 2.1; fig. 43). In contrast, the caudalmost portion of the maxilloturbinat is simple in morphology with few branches and scrolls and is attached to the nasal cavity wall or floor in all other mammals I examined (character 2.0; fig. 43).

The rostral portion of endoturbinat I is ventral to the maxilloturbinat in Vombatiformes (character 16.1; fig. 44), whereas in all other mammals I examined the rostral

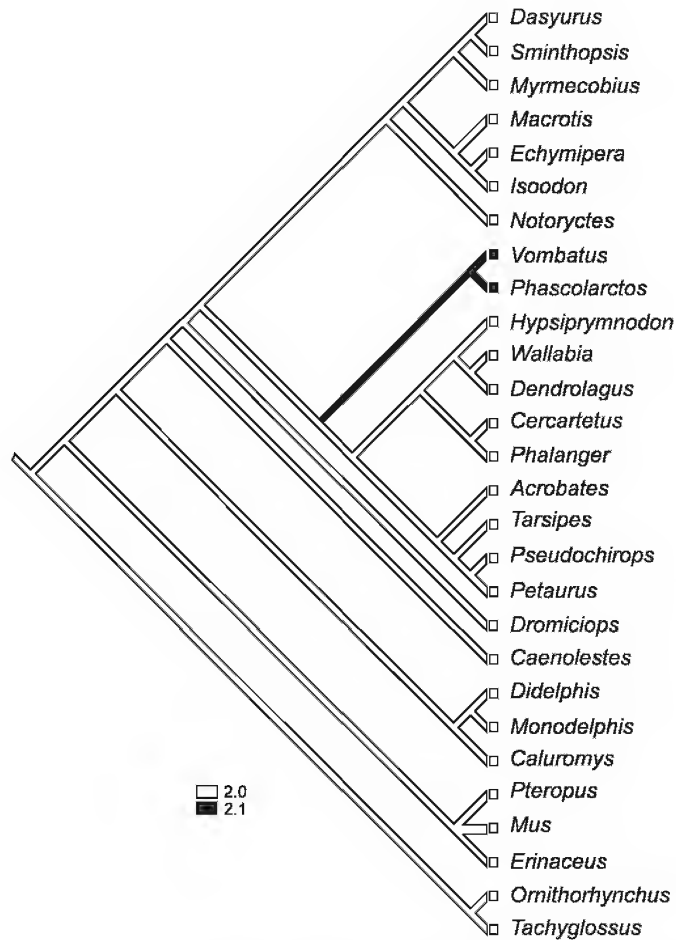


Fig. 43. Character 2 (morphology of the caudalmost portion of the maxilloturbinal) optimized on the Meredith et al. (2009) topology. For character state 2.0, the caudal maxilloturbinal is simple in morphology and is attached to the nasal cavity wall or floor. For character state 2.1, the caudalmost portion of maxilloturbinal becomes an enclosed tube that tapers into a cone that is unattached to the nasal cavity. States for this character are illustrated in figure 38.

portion of endoturbinal I overlies the maxilloturbinal (character 16.0; fig. 44; Rowe et al., 2005).

The morphology of the maxilloturbinal and its relationship to endoturbinal I in the koala and wombat are very different from that of any other mammal. The caudal portion of the maxilloturbinal and the corresponding respiratory epithelium attached to this element (Kratzing, 1984) overlie the rostral portion of endoturbinal I in the vombatiformes contra the condition in other marsupials and mammals in general. The functional significance of this relation-

ship is unclear. The koala and wombats are different ecologically, with the former arboreal and the latter terrestrial (Nowak, 1999). This suggests that the derived morphology found in the two taxa of extant vombatiformes is not driven by ecology and instead may result from shared ancestry. Examination of the maxilloturbinal in fossil vombatiformes (e.g., Diprotodontidae, Ilariidae) is required to test this hypothesis.

The presence of two ectoturbinals (character 19.1; fig. 45) is the ancestral condition for Marsupialia and also an equivocal synapomorphy for the clade. There are

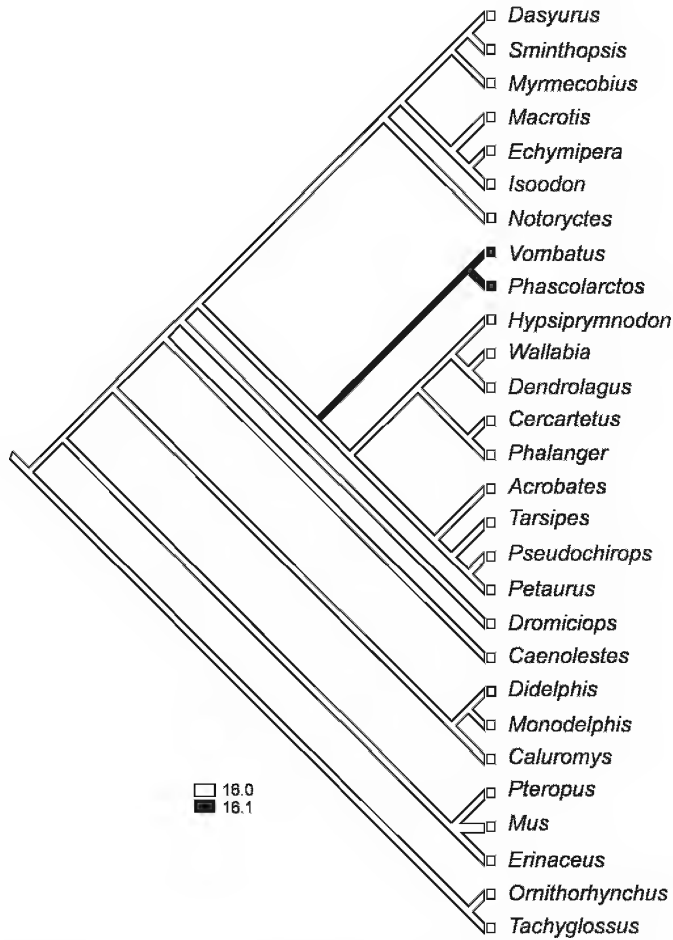


Fig. 44. Character 16 (presence or absence of rostral portion of endoturbinal I) optimized on Meredith et al. (2009) topology. For character state 16.0, the rostral portion of endoturbinal I is present. For character state 16.1, the rostral portion is absent. States for this character are illustrated in figure 39.

several deviations from this number among marsupials and the placental *Erinaceus* also has two ectoturbinals (appendix 3). There were no major discrepancies in the distributions of the character states discussed thus far on the two topologies for marsupial relationships (figs. 1 and 2). However, I found one character that supported the placement of *Dromiciops* as the sister taxon to all Australasian marsupials (character 11.1; fig. 46), which is consistent with the topology of Meredith et al. (2009; fig. 1), and contra the placement of *Dromiciops* as the sister taxon to Diprotodontia found by Sánchez-Villagra et al. (2007; fig. 2). Ultimately, the characters that I document in this paper for marsupials need to be

explored in other groups of mammals. Some of these character states may be diagnostic for groups outside Marsupialia or potentially diagnostic for more inclusive groups of mammals. I encourage others to incorporate the new characters described here in future phylogenetic analyses containing matrices that more broadly sample marsupial anatomy.

Ancestral Reconstruction of Number of Turbinals

Presence of five endoturbinals and two ectoturbinals appears to be the ancestral condition for Marsupialia based on this sample of extant taxa (fig. 47). The nonmarsupial metatherians for which CT imagery is published for the skull include *Pucadelphys*

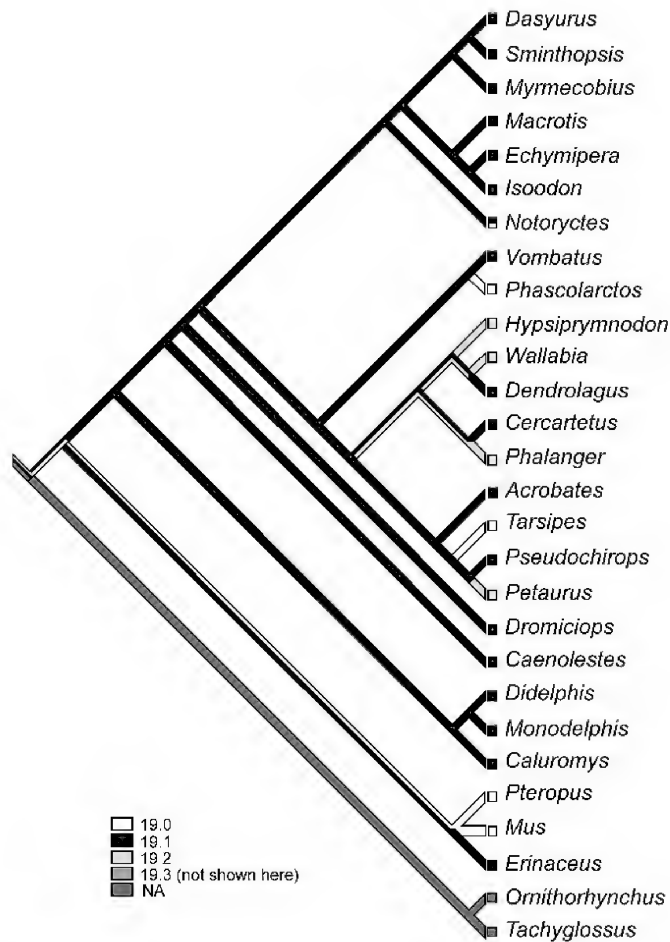


Fig. 45. Character 19 (number of ectoturbinals) optimized on Meredith et al. (2009) topology. Character state 19.0 is the presence of one ectoturbinal; 19.1 is the presence of two ectoturbinals; 19.2 is the presence of three ectoturbinals; 19.3 is the presence of four ectoturbinals (this state is not shown on this tree). States for this character are illustrated in figure 21. Abbreviation: NA, not applicable.

andinus (Macrini et al., 2007a), and *Herpetotherium fugax* (Horovitz et al., 2008). One specimen of *Herpetotherium* preserves a broken ossified nasal septum and a partial posterior transverse lamina, but otherwise not much data are obtainable from the internal nasal cavities of these taxa. The turbinal characters presented in this paper cannot be scored using these taxa nor can the number of turbinal elements be determined at this time. So, at present, the ancestral number of turbinals for Metatheria is uncertain.

The number of endoturbinals and ectoturbinals for different placental mammals is variable, ranging from those taxa with two or

three endoturbinals (e.g., *Callithrix jacchus* [Smith et al., 2004]; *Pteropus lylei* [Giannini et al., in review]) and those with one or no ectoturbinals (e.g., *Rhinolophus rouxii*, [Stöbel et al., 2010]; *Pteropus lylei* [Giannini et al., in review]), to 10 endoturbinals and 16 ectoturbinals in pigs (Paulli, 1900b; Moore, 1981). Some fully aquatic placental mammals (e.g., some odontocete cetaceans) lack ossified endo- and ectoturbinals altogether (Edinger, 1955; Ridgway et al., 1987; Colbert et al., 2005). Based on this much diversity, it is difficult to reconstruct the ancestral numbers of turbinal elements for Placentalia. Efforts should first concentrate on determining the

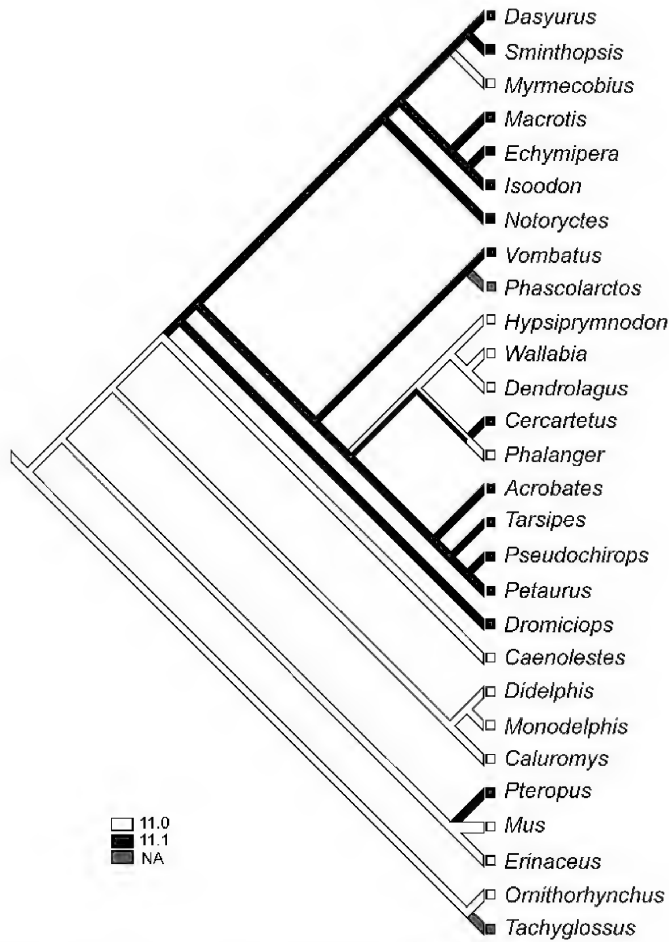


Fig. 46. Character 11 (presence or absence of an uncinat process of nasoturbinale) optimized on Meredith et al. (2009) topology. Character state 11.0 is the presence of an uncinat process; 11.1 is the absence of the uncinat process. States for this character are illustrated in figure 14. Abbreviation: NA, not applicable.

number of elements in various placental clades using broad taxonomic sampling (e.g., Chiroptera, Allen, 1882).

The ancestral number of endoturbinals and ectoturbinals for Monotremata is unclear because the number of elements is very different in the two clades of extant monotremes. *Ornithorhynchus anatinus*, the platypus, has two endoturbinals and no ectoturbinals, whereas *Tachyglossus aculeatus*, the short-snouted echidna, has 18 endoturbinals and no ectoturbinals based on the usage of the terms in my paper (fig. 18; table 7; data from Paulli, 1900a). This huge discrepancy between the platypus and echidnas was possibly driven by differences in ecology;

Ornithorhynchus is mostly aquatic, whereas *Tachyglossus* is terrestrial (Griffiths, 1978). Consequently, the platypus relies on olfaction less than echidnas, as is the case in other aquatic mammals. The olfactory bulbs are reduced in size compared to the whole brain in the platypus relative to echidnas (Pirrot and Nelson, 1978; Macrini et al., 2006), and there are roughly only one half as many odorant receptor genes in the platypus genome compared to other mammals (Warren et al., 2008). Perhaps a reduction in the number of genes coding for turbinals in the platypus relative to the ancestral condition in mammals combined with a duplication event in the homologous portion of the genome in

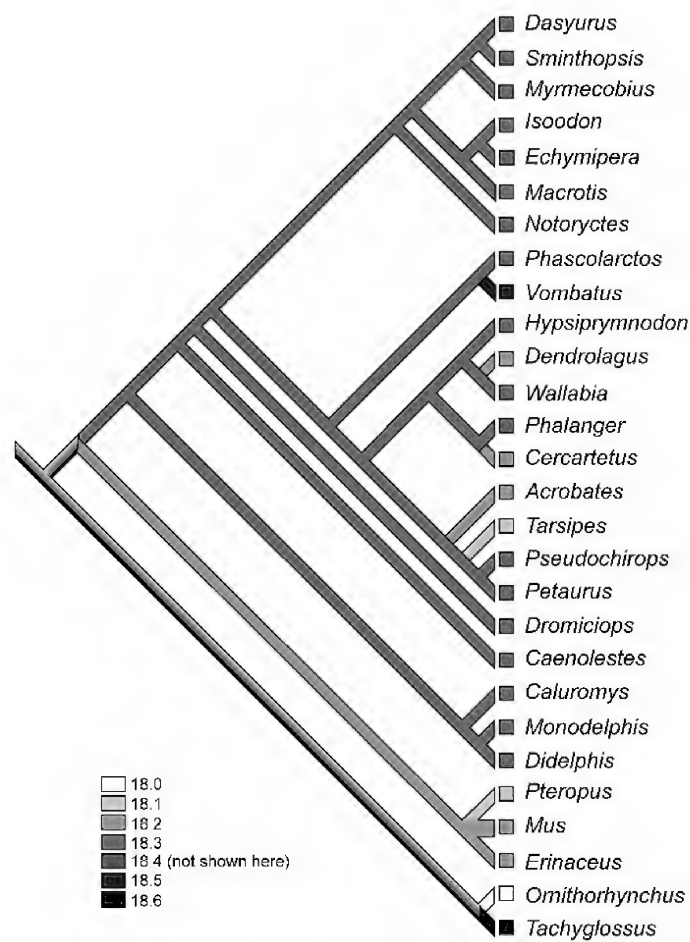


Fig. 47. Character 18 (number of endoturbinals) optimized on Meredith et al. (2009) topology. Character state 18.0 is the presence of two endoturbinals; 18.1 is the presence of three endoturbinals; 18.2 is the presence of four endoturbinals; 18.3 is the presence of five endoturbinals; 18.4 is the presence of six endoturbinals; 18.5 is the presence of seven endoturbinals; 18.6 is the presence of more than seven endoturbinals. States for this character are illustrated in figure 18.

TABLE 7
Number of endoturbinals and ectoturbinals for outgroup species examined

Species	Higher taxon	Specimen No.	No. Endo	No. Ecto
<i>Ornithorhynchus anatinus</i> *	Ornithorhynchidae	AMNH 200255	2	0
<i>Tachyglossus aculeatus</i> *	Tachyglossidae	AMNH 154457	18	0
<i>Pteropus lylei</i>	Pteropodidae	AMNH 237593	3	1
<i>Mus musculus</i>	Murinae	TMM M-3196	4	1
<i>Erinaceus</i> sp.	Erinaceidae	uncataloged	4	2

Abbreviations: *, Number of turbinal elements in *Ornithorhynchus* and *Tachyglossus* based on data from CT images and Paulli (1900a).

Tachyglossus is the mechanism responsible for the differences in turbinal number in these two monotremes.

This number of turbinal elements is fairly well conserved in marsupials compared to placentals and monotremes, with both of the latter two groups showing a greater amount of within-clade variation. Although the number of ecto- and endoturbinals vary between species of mammals, the presence of an ossified maxilloturbinal and nasoturbinal appears to be highly conserved. The exceptions are the fully aquatic mammals such as the cetaceans, many of which lack olfactory bulbs, ossified turbinals, and a cribriform plate altogether (Edinger, 1955; Ridgeway et al., 1987; Colbert et al., 2005).

The ancestral number of endoturbinals and ectoturbinals for Mammalia is unclear because of the great amount of variation among the three major extant clades of mammals. In addition, the interiors of nasal cavities of fossil mammals are rarely preserved in good enough condition to allow for extensive study of the turbinals. For example, well-preserved turbinal elements have not been described for a multituberculate mammal, a speciose clade of stem therians known from the Mesozoic and early Tertiary of nearly every continent (Kielan-Jaworowska et al., 2004). However, remnants of ossified turbinals were noted in some multituberculates (Kielan-Jaworowska et al., 1986; Hurum, 1994; Wible and Rougier, 2000; Macrini, 2006).

There is no direct evidence for ossified turbinals in taxa outside of crown Mammalia. Some have suggested that ridges on the internal surfaces of the nasal cavity of therocephalians, a lineage of nonmammalian therapsids that is the sister taxon to cynodonts, served for attachment of turbinal elements (Hillenius, 1994). However, the interpretation of these ridges is debated in the literature (e.g., Kemp, 2006) and there are no preserved ossified turbinals in these specimens. Furthermore, ossified turbinals were not observed in key nonmammalian cynodont taxa (e.g., *Hadrocodium wui*; Macrini, 2006; Rowe et al., 2011) that are closely related to crown Mammalia. Therefore, the presence of these ossified elements is currently considered a synapomorphy for crown

Mammalia (e.g., Rowe, 1988; Luo et al., 2007).

Comparisons of Turbinals with Ecological Characteristics

I obtained ecological data (habitat use, diet, and activity pattern) from the literature (Nowak, 1999) for each of the marsupial species examined in this study (table 8). These data were compared with the number of turbinal elements as a preliminary examination of ecological correlates for morphological differences of the ethmoid and associated internal nasal cavity osteology between marsupial species. I examined the number of endoturbinals and ectoturbinals because these elements are primarily associated with olfactory epithelium (e.g., Rowe et al., 2005) and because the other bony turbinal elements (maxilloturbinal and nasoturbinal) are each present in all species examined. Furthermore, the maxilloturbinal and a portion of the nasoturbinal, including the variably present rostral nasoturbinal, are covered by respiratory epithelium in at least some marsupials (e.g., *Monodelphis domestica*, Rowe et al., 2005) and would not be expected to show the same relationships with these ecological variables as the other turbinal elements that are covered with olfactory epithelium.

There are no obvious trends in activity patterns and the number of ectoturbinals, endoturbinals, or combined elements for these marsupials, as all but two species are nocturnal. Similarly, there are no obvious patterns in habitat use and numbers of any of the groups of turbinals.

However, there appears to be some pattern in diet with the number of combined ectoturbinals and endoturbinals. *Tarsipes*, which has the fewest number of ectoturbinals and endoturbinals at four, has a diet consisting of pollen, nectar, and insects (Nowak, 1999). The snout of *Tarsipes* is long and slender, an adaptation for animals that feed on pollen and nectar, and so it is possible that the shape of the nasal cavity is a primary constraint on the number of turbinal elements.

Sarcophilus, a scavenger (Nowak, 1999), has the greatest number of ectoturbinals and endoturbinals at 10. The presence of a large number of turbinal elements that are

TABLE 8
Data (from Nowak, 1999) on habitat, diet, and daily activity for marsupial species used in this study

Species	Habitat	Diet	Activity
<i>Acrobates pygmaeus</i>	arboreal	insectivorous	nocturnal
<i>Caenolestes fuliginosus</i>	terrestrial	insectivorous	nocturnal
<i>Caluromys philander</i>	arboreal	omnivorous	nocturnal
<i>Cercartetus caudatus</i>	arboreal	insectivorous	nocturnal
<i>Dasyurus hallucatus</i>	terrestrial	carnivorous	nocturnal
<i>Dendrolagus lumholtzi</i>	arboreal	herbivorous	nocturnal
<i>Didelphis virginiana</i>	terrestrial	omnivorous	nocturnal
<i>Dromiciops gliroides</i>	arboreal	insectivorous	nocturnal
<i>Echymipera kalubu</i>	terrestrial	omnivorous	nocturnal
<i>Hypsiprymnodon moschatus</i>	terrestrial	mainly insectivorous	diurnal
<i>Isodon macrourus</i>	terrestrial	omnivorous	nocturnal
<i>Macrotis lagotis</i>	terrestrial	omnivorous	nocturnal
<i>Monodelphis domestica</i>	terrestrial	omnivorous	nocturnal
<i>Myrmecobius fasciatus</i>	terrestrial	insectivorous	diurnal
<i>Notoryctes typhlops</i>	fossorial	insectivorous	nocturnal
<i>Petauroides volans</i>	arboreal	folivorous	nocturnal
<i>Petaurus breviceps</i>	arboreal	omnivorous	nocturnal
<i>Phalanger orientalis</i>	arboreal	folivorous and frugivorous	nocturnal
<i>Phascogale carolinensis</i>	arboreal	herbivorous	nocturnal
<i>Potorous tridactylus</i>	terrestrial	omnivorous	nocturnal
<i>Pseudocheirus occidentalis</i>	arboreal	mainly folivorous	nocturnal
<i>Pseudochirops cupreus</i>	arboreal	mainly folivorous	nocturnal
<i>Sarcophilus harrisii</i>	terrestrial	scavenger	nocturnal
<i>Sminthopsis crassicaudata</i>	terrestrial	insectivorous	nocturnal
<i>Tarsipes rostratus</i>	terrestrial	pollen, nectar, insects	nocturnal
<i>Thylacinus potens</i>	terrestrial	carnivorous	nocturnal
<i>Trichosurus vulpecula</i>	arboreal	herbivorous	nocturnal
<i>Vombatus ursinus</i>	terrestrial	herbivorous	nocturnal
<i>Wallabia bicolor</i>	terrestrial	herbivorous	nocturnal

complexly branching, convoluted, and densely packed in the nasal cavity (char. state 14.1, appendix 2) is consistent with the condition of these elements in placental scavengers such as *Crocota crocota*, the spotted hyena (Owen, 2001).

Conclusions

The ethmoids of marsupials are fairly conserved in terms of the number of turbinal elements present. Each taxon examined has an ossified maxilloturbinal, nasoturbinal, at least one ectoturbinal, and at least three endoturbinals, but typically marsupials have five endoturbinals and two ectoturbinals, and this appears to be the ancestral condition for Marsupialia (table 4). However, there is considerable variation in the morphology of

the bony turbinals and in the placements of the lamellae of these elements.

I documented much of the observed variation in the nasal cavity using 35 morphological characters (appendix 2). Examination of these characters on preexisting topologies of marsupial relationships revealed some phylogenetic signal for my sample of marsupial species. Three of the 35 characters are punitively diagnostic for previously recognized clades within Marsupialia. It is possible that, when my matrix (appendix 3) is combined with morphological data from other anatomical systems and molecular data, previously unrecognized or controversial clades within Marsupialia may be supported.

Alternatively, much of the interspecific variation in the osteology of the ethmoid may result from developmental or ecological

factors. My preliminary comparison of ecological data and morphological differences did not suggest many correlations. However, previous studies found that aquatic carnivorans have a significantly decreased surface area for olfactory epithelium than terrestrial carnivorans (Van Valkenburgh et al., 2011), and that there is a correlation between ecological use and number of olfactory receptor genes in mammals in general (Hayden et al., 2010). Perhaps correlations between ecological and morphological characters would be more apparent if quantitative data, such as surfaces areas for turbinals that support different types of epithelium (e.g., Van Valkenburgh et al., 2004) or morphometric data from within the nasal cavity (e.g., Márquez and Laitman, 2008), are compared rather than discrete data (e.g., number of turbinal elements). It is also possible that the differences in turbinal elements in marsupials are correlated with differences in body sizes. The size of the olfactory organ, as measured by the surface area of the cribriform plate, generally scales with skull size in mammals (Pihlström et al., 2005). However, the turbinal elements have not been explicitly compared with body size for any group of mammals.

The documentation of the number of turbinals in different species of marsupials in this paper (table 4) provides some basic data necessary for studying the underlying causes of diversity in the complexity of the ethmoid between different species of mammals. Furthermore, my study highlights some issues with homologies of mammalian nasal cavity elements that need to be resolved.

Specifically, there needs to be a more in-depth examination of the development of endoturbinals and ectoturbinals to test the current view of serial/iterative homology among these groups of elements. There are distinctive differences between the five endoturbinals that are present in the generalized adult marsupial condition. Specifically, endoturbinals II and IV tend to have relatively few if any branches in most marsupials examined in this study, whereas endoturbinals III and V are typically bifurcating elements with both branches terminating in turbinal folds. This fairly conserved

adult pattern needs to be traced in developmental series for these taxa to determine whether differences can be recognized that might suggest some (or all) of these elements are in fact individualized and not serially homologous. Preliminary work revealed that endoturbinal III consistently appears later in postnatal ontogeny than any of the other four endoturbinals in the didelphid marsupials *Caluromys philander* (Macrini and Sánchez-Villagra, 2008), *Monodelphis domestica* (Freyer, 1999), and *Didelphis marsupialis* (Toeplitz, 1920). This suggests that at least some of the turbinal elements have distinctive ontogenies that can be traced across different taxa. Hence, perhaps not all turbinal elements should be assumed to be serially homologous.

Regardless, the underlying genetic pathways responsible for turbinal development need to be documented to test the current view of serial homology of endoturbinals and ectoturbinals. In addition, it would be interesting to test whether duplication or deletion events of olfactory coding genes are correlated with the number of turbinal elements. Little has been done to correlate specific genes with osteological turbinal elements, but at least now the genome of one species of marsupial, *Monodelphis domestica*, is completely sequenced (Mikkelsen et al., 2007). As the olfactory coding genes are documented for more marsupials, it will be possible to examine the relationship between the olfactory portions of the genome with the anatomy of the ethmoid. But this would not be possible were the gross anatomy of the marsupial ethmoid not documented first.

Finally, a reexamination of the ossification of the nasal septum in marsupials (and other mammals; see Ferigolo, 1981) is warranted to determine whether this element arises from an ossification center of the presphenoid (Broom, 1926, 1927, 1935), or it proceeds from a separate, more rostral ossification center and therefore should be called a mesethmoid (Rowe et al., 2005). The development of the ossified nasal septum has been documented in only a handful of marsupial species (e.g., Broom, 1926; Clark and Smith, 1993) and needs to be more thoroughly documented to resolve this issue.

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APPENDIX 1

TERMINOLOGY FOR OSTEOLOGICAL STRUCTURES
DESCRIBED FROM ADULT SKULLS

Cribriform plate: The cribriform plate (lamina cribrosa: NAV, 2005) is the caudal portion of the ethmoid that forms the rostral wall of the endocranial cavity (fig. 23). As its name suggests, the cribriform plate is perforated by a number of olfactory foramina that allow passage of bundles of the fibers of the olfactory nerve (fila olfactoria). In addition, a large dorsomedial opening in the plate called the cribroethmoidal foramen allows passage of the anterior ethmoidal nerve (Wible, 2008). Typically, all the bony turbinal elements except for the maxilloturbinal coalesce caudally to provide contributions to the cribriform plate (Allen, 1882; Rowe et al., 2005). The surface of the cribriform plate that faces the endocranial cavity is called the *encranial surface* (Allen, 1882). The encranial surface consists of perforate and imperforate portions (Allen, 1882). The perforate portion corresponds with the ectoturbinals, dorsalmost endoturbinals, and the septoturbinal space. The imperforate portion of the encranial surface corresponds with the ventralmost endoturbinals (Allen, 1882).

Crista galli: The crista galli is the portion of the ossified nasal septum that penetrates the cribriform plate into the endocranial cavity, forming a midsagittal crest that projects caudally for a short distance between the olfactory bulbs of the brain (fig. 23; Allen, 1882; Rowe et al., 2005).

Ectoturbinal: I use the term *ectoturbinal* (ectoturbinalia: NAV, 2005) as defined by Allen (1882) for turbinal elements whose attachments are in the interspace between the nasoturbinal and endoturbinal I (fig. 21; Allen, 1882). In contrast, Paulli (1900a, 1900b, 1900c) refers to ectoturbinals as any turbinal element that does not closely approach the nasal septum, including those located beneath the interspace between the nasoturbinal and endoturbinal I. The degree to which a turbinal element approaches the midline is a continuous value and consequently the distinction between ectoturbinals and endoturbinals following Paulli (1900a, 1900b, 1900c) is arbitrary. Conversely, endoturbinal I is easily recognized in marsupials and most other mammals by its morphology, and therefore the definition of Allen (1882) can be applied readily across Mammalia. The ectoturbinals and endoturbinals are also distinguished from each other by their development. The ectoturbinals form as folds of the pars intermedia in the developing chondrocranium, whereas the endoturbinals develop from folds in the pars posterior (Smith and Rossie, 2006).

Ectoturbinals are named by Arabic numbers from anterodorsal to posteroventral in the nasal cavity based on the position of the respective bases of these elements, such that the base of ectoturbinal 1 is dorsal to that of ectoturbinal 2 (fig. 21). This numbering

scheme reflects the current view that ectoturbinals are serially homologous. The ectoturbinals are also referred to as *frontoturbinals* (e.g., Maier, 1993a), particularly the cartilaginous precursors, and *secondary ethmoturbinals* (Jurgens, 1963). Ectoturbinal I was named the *upper turbinal* by Parker (1874) in his description of the skull of the pig.

Endoturbinal: The endoturbinals (endoturbinalia: NAV, 2005) are distinct from the other turbinal elements in several aspects. Following the definition of Allen (1882), the endoturbinals lie beneath the ectoturbinals (fig. 18). The endoturbinals (other than endoturbinal I) form as folds of the pars posterior in the developing chondrocranium, whereas the ectoturbinals develop from folds of the pars intermedia (Smith and Rossie, 2006).

The endoturbinals span the entire height of the sphenethmoidal recess (Rowe et al., 2005). The distal ends of endoturbinals coalesce to form the ethmoid plate of the posterior transverse lamina and the bases of the endoturbinals come together to form the roof of the sphenethmoid recess around the olfactory bulbs (Rowe et al., 2005). The upper surface of each endoturbinal is the frontal border and the lower surface is called the palatal border (Allen, 1882).

Endoturbinals are named using Roman numerals from anterodorsal to posteroventral in the nasal cavity based on the position of the respective bases of these elements, such that the base of endoturbinal I is dorsal to that of endoturbinal II. Paulli (1900a, 1900b, 1900c) numbers the nasoturbinal as endoturbinal I (fig. 17). However, other authors (e.g., Allen, 1882; Bhatnagar and Kallen, 1974b; Rowe et al., 2005) refer to endoturbinal I as the element with its base caudal and ventral to the dorsal attachment of the nasoturbinal (figs. 17 and 18).

In this paper, I chose the convention of Allen (1882) over Paulli (1900a, 1900b, 1900c) (fig. 17) because the numbering convention for endoturbinals of Allen (1882) is more consistent with the literature on the development of the nasal capsule (e.g., Voit, 1909; Maier, 1993a, 2000; Freyer, 1999). Ethmoturbinal I of the developmental literature is equivalent with endoturbinal I of Allen (1882) (table 3). The nasoturbinal is also distinct from the endoturbinals in development; the former develops mostly from tectal cartilage and the pars anterior as well as the ossification of the crista semicircularis, whereas the latter form as folds of the pars posterior (Smith and Rossie, 2006).

Endoturbinal I (concha nasalis media: NAV, 2005) is generally a very conspicuous element in mammals with its rostralmost extremity forming a ventrally concave roof over the maxilloturbinal. In *Monodelphis domestica*, endoturbinal I forms a partition between the olfactory (above) and respiratory (below) portions of the nasal cavity (Rowe et al., 2005). In the development of the cartilaginous nasal capsule, the pars posterior medially overlaps the caudal portion of the pars intermedia; the ossification of this overlap is endoturbinal I (fig. 8; Rossie, 2006). Endoturbinal I was also called the *middle turbinal* by Parker (1874) in his description of the skull of the pig.

Endoturbinals below endoturbinal I (e.g., endoturbinal II, III, IV, etc.) are considered serially homologous because these endoturbinals chondrify as rudiments of successive endoturbinals (fig. 8), are identified solely on their relative position, and the number of these elements is variable within species (Rowe et al., 2005; Rossie, 2006, 2008).

The endoturbinals are also sometimes referred to as *ethmoturbinals* (e.g., Voit, 1909; Maier, 1993a; Freyer, 1999; table 3), particularly the cartilaginous precursors; although other authors (e.g., Negus, 1958; Bhatnagar and Kallen, 1974b; Moore, 1981) use the term *ethmoturbinal* to refer to both the endoturbinals and the ectoturbinals. Because of this confusion in the literature over the term *ethmoturbinal*, I use the term *endoturbinal* here. In addition, ontogenetic series are not available for all of the taxa I examined in this paper, and therefore I cannot determine whether the ossified elements in the adult skull develop from *ethmoturbinals* (as the term is used in reference to the cartilaginous precursors) or *interturbinals*. An *interturbinal* is an element that develops after all the other endoturbinals are present, and usually forms between preexisting turbinal elements (*sensu* Maier, 1993b, 2000; Freyer, 1999). Furthermore, in the literature the term *endoturbinal* is applied only to the ossified structures visible in the adult skull and my application of the term here is consistent with this usage.

Ethmoid: The ethmoid bone (*os ethmoidale*: NAV, 2005) is a complex mass of paired, perichondral ossifications in the nasal cavity of mammals (fig. 5). Some authors (e.g., Moore, 1981) consider the ethmoid to consist of the bony ecto- and endoturbinals only, whereas others (NAV, 2005) also include the nasoturbinal as part of the ethmoid. I consider the maxilloturbinal, nasoturbinal, ectoturbinals, and endoturbinals to be part of the ethmoid (*sensu* Rowe et al., 2005; fig. 5). Although each of these elements have different developmental histories, they all arise in the epithelium of the nasal cavity (Rowe et al., 2005), and these are the only turbinal elements to ossify in the mammalian skull. Furthermore, these turbinals are always found together as ossified elements of the adult mammalian skull; there are no instances in which any one of these elements is not ossified in adults whereas the others are ossified.

Coalescence of the caudal portions of the ectoturbinals, endoturbinals, and nasoturbinal forms the cribriform plate of the ethmoid (fig. 23; Allen, 1882; Rowe et al., 2005). In the adult skull, portions of the ethmoid are fused to various other elements of the nasal skeleton, such as the ossified nasal septum, nasals, maxillae, vomer, and frontals.

Ethmoid plate: The ethmoid plate (basal plate: Negus, 1958) is the portion of the posterior transverse lamina that is formed by the coalescence of the rostral endoturbinals (Rowe et al., 2005). The ventralmost ectoturbinal sometimes contacts the rostral portion of the ethmoid plate. The ethmoid plate combines with the parasseptal shelf of the vomer to form the posterior transverse lamina.

Frontal recess: The frontal recess (*recessus frontalis*: Maier, 1993a; Rossie, 2006) is the dorsal portion of the lateral recess that is bounded ventrally by the root of endoturbinal I (fig. 25). The frontal recess houses the ectoturbinals. If secondary pneumatization occurs ontogenetically in the frontal bone surrounding the recess, this space becomes known as the frontal sinus (fig. 25; Rossie, 2006).

Lateral recess: The lateral recess (*recessus lateralis*: Maier, 1993a; Rossie, 2006) forms in the chondrocranium from the overlap of components of the lateral wall of the nasal capsule (*paries nasi*) (figs. 8, 48, and 49). Namely, the caudal portion of the pars anterior medially overlaps the rostral portion of the pars intermedia to form the crista semicircularis, which typically ossifies as the caudal portion of the nasoturbinal in the adult skull (fig. 8; Fawcett, 1917; de Beer, 1937; Rossie, 2006). The pars posterior medially overlaps the caudal portion of the pars intermedia to form the base of endoturbinal I (Rossie, 2006). The crista semicircularis and endoturbinal I effectively form the medial wall of the lateral recess, whereas the pars intermedia forms the lateral wall (Rossie, 2006). The lateral recess may become further divided into a dorsal and ventral space by the root of endoturbinal I; the dorsal space is known as the *frontal recess*, which contains the ectoturbinals, and the ventral space is known as the *maxillary recess*. The usage of *lateral recess* here is equivalent to the usage of *maxillary sinus* in Rowe et al. (2005). The lateral recess is homologous to the middle meatus of humans (Rossie, 2006).

Maxillary recess: The maxillary recess (*recessus maxillaris*: NAV, 2005) is the ventral portion of the lateral recess that is bounded dorsally by the root of endoturbinal I (figs. 26 and 27). If during ontogeny secondary pneumatization occurs in the maxilla surrounding the recess, this space becomes known as the maxillary sinus (Rossie, 2006).

Maxilloturbinal: The maxilloturbinal (*os conchae nasalis ventralis*: NAV, 2005) is the rostralmost ossified turbinal element in the nasal cavity, which is attached to the medial surface of the maxilla (figs. 5, 7, 28, and 37). The maxilloturbinal develops from an involution of the ventral margin of the *paries nasi* (Voit, 1909; de Beer, 1937; Klutzny, 1994; Freyer, 1999; Maier, 2000; da Silva Neto, 2000). It is covered by respiratory epithelium in *Monodelphis domestica* (Rowe et al., 2005). The maxilloturbinal is also known as the *lower turbinal* in the pig (Parker, 1874), and the *inferior nasal concha* in human anatomy (Moore, 1981).

Nasal cavity: The bilateral space within the skull of a mammal, which is rostral to the cribriform plate, is called the nasal cavity (*cavum nasi*: NAV, 2005). The nasal cavity comprises the paired nasopharyngeal meatus and sphenethmoid recess. The nasal septum divides the nasal cavity medially into right and left chambers. From rostral to caudal, the paired premaxilla, maxilla, nasal, lacrimal, frontal, palatine, and

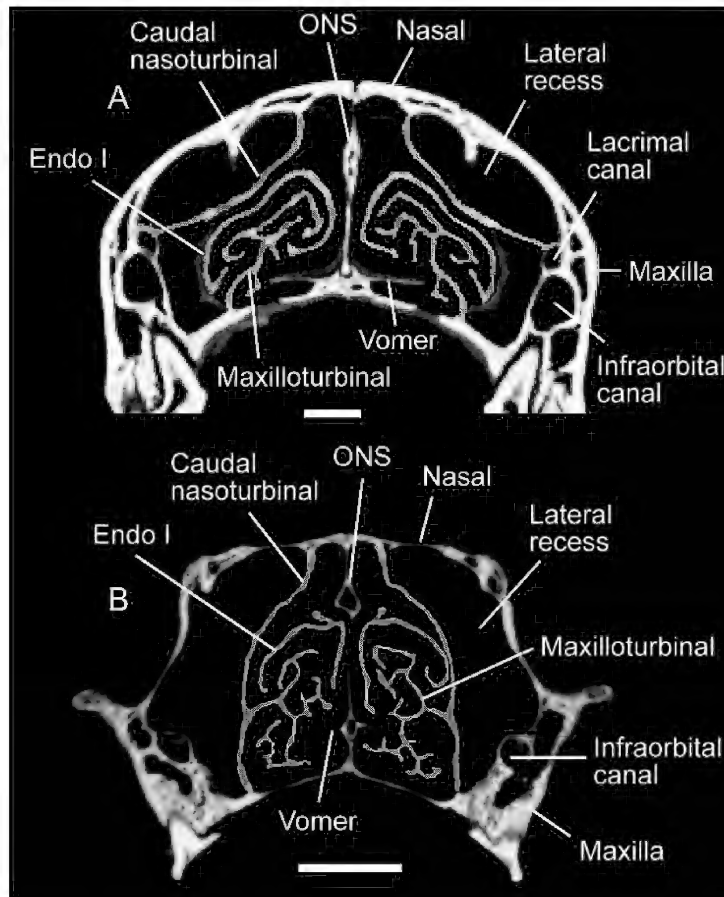


Fig. 48. Coronal CT images showing the dorsoventral extent of caudal portion of lateral recess (char. 23). (A) lateral recess does not extend to nasal cavity floor (char. 23.0), *Monodelphis domestica*, C158 (TMM M-7599), scale bar equals 1 mm; (B) lateral recess extends to the floor of the nasal cavity (ch. 23.1), *Petauroides volans*, C405 (AMNH 150055), scale bar equals 5 mm. Abbreviations: Endo, endoturbinale; ONS, ossified nasal septum.

orbitosphenoid bones contribute to the dorsal, lateral, and ventral walls of the nasal cavity in mammals (fig. 3). The septomaxilla also contributes to the nasal cavity in extant monotremes, some extinct groups of crown mammals (e.g., eutriconodontids), and possibly a fossil eutherian (Hu et al., 2010). The rostral portion of the nasal cavity is not bounded by bone, but is marked by the external nares. The cribriform plate of the ethmoid forms the antero-caudal wall of the nasal cavity and the caudalmost portion of the sphenethmoid recess extends into the orbitosphenoid bone and is roofed by the cribriform plate.

Nasopharyngeal meatus: The nasopharyngeal meatus (meatus nasopharyngeus; NAV, 2005) is the space located ventral to the posterior transverse lamina that is devoid of turbinal folds and extends caudally to the choanae (sensu Moore, 1981; fig. 6). The meatus is

lined with respiratory epithelium in *Monodelphis domestica* (Rowe et al., 2005). The term *nasopharyngeal passageway* is sometimes used synonymously with nasopharyngeal meatus (Rowe et al., 2005).

Nasoturbinal: The nasoturbinal (concha nasalis dorsalis; NAV, 2005) is a complex and compound structure in the mammalian skull (fig. 5). In this paper, I recognize the nasoturbinal as consisting of two parts, the rostral and caudal nasoturbinal. The rostral nasoturbinal corresponds with a compound structure developing from a medial contribution from the ventral folding of the tectum and a lateral contribution formed from a portion of the pars anterior (Smith and Rossie, 2006). The ossification of this compound structure forms the rostral nasoturbinal in adult skulls. In marsupial skulls, the rostral nasoturbinal is represented as a bony process that projects ventrally into the nasal cavity (figs. 9 and 10).

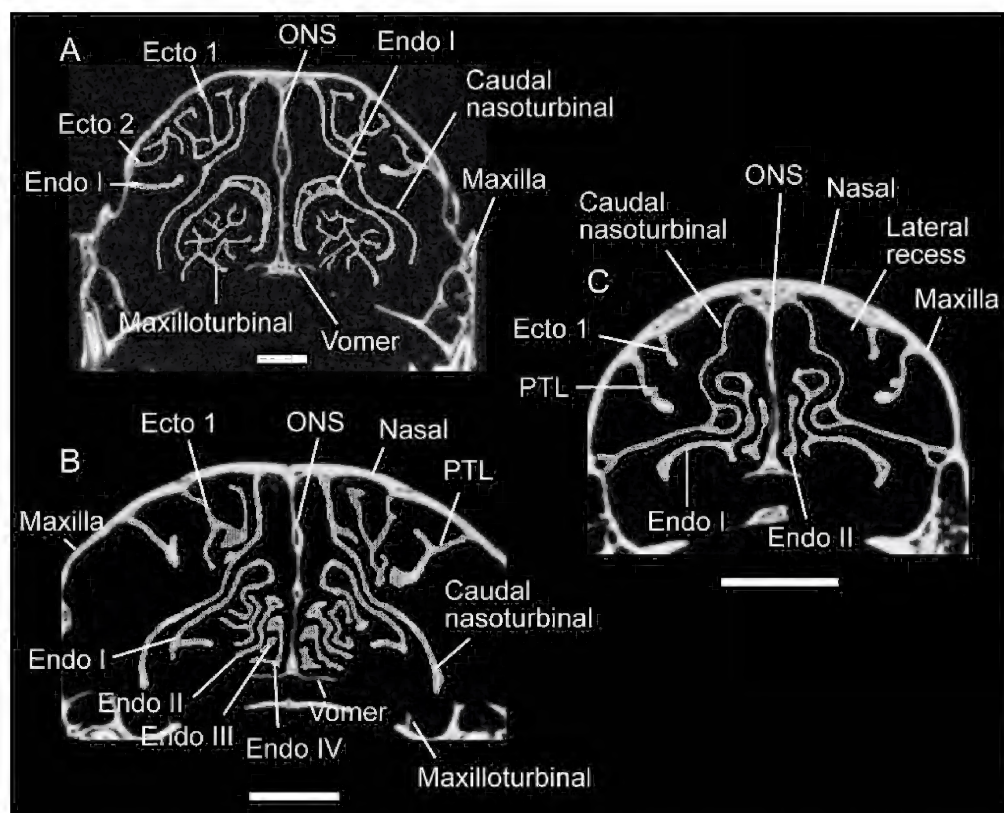


Fig. 49. Coronal CT images showing the caudal extent of lateral recess (char. 24). (A) rostral in the snout, maxilloturbinal extends caudal to lateral recess (char. 24.0), *Dromiciops gliroides*, C230 (FMNH 127463), scale bar equals 1 mm; (B) lateral recess extends about even with the caudal terminus of the maxilloturbinal (char. 24.1), *Dasyurus hallucatus*, C286 (TMM M-6921), scale bar equals 5 mm; (C) lateral recess extends caudal to the maxilloturbinal (char. 24.2), *Isoodon macrourus*, C360 (TMM M-6922), scale bar equals 5 mm. Abbreviations: Ecto, ectoturbinal; Endo, endoturbinal; ONS, ossified nasal septum; PTL, posterior transverse lamina.

The rostral nasoturbinal is equivalent to the nasoturbinal in the literature describing the development of the nasal cavity (e.g., Voit, 1909; Maier, 1993a, 2000; Freyer, 1999).

The caudal nasoturbinal of this paper corresponds to the ossification of the crista semicircularis (fig. 8). The crista semicircularis forms in the chondrocranium of mammals from the overlap of the caudal portion of the pars anterior and the rostral portion of the pars intermedia of the paries nasi (fig. 8; Voit, 1909; de Beer, 1937; Maier, 1993a, 2000; Freyer, 1999; da Silva Neto, 2000; Rossie, 2006). The projection of the caudal portion of the pars anterior into the nasal capsule is the crista semicircularis. The crista semicircularis forms part of the medial border of the lateral recess (fig. 8; Rossie, 2006). The crista semicircularis often ossifies in the mammalian adult skull, particularly marsupials (figs. 11–13, 35). This structure is what the literature on the adult mammalian skull typically calls the nasoturbinal (e.g., Sharma,

1958; Bhatnagar and Kallen, 1974b; Kratzing, 1978; Rowe et al., 2005).

The rostral nasoturbinal is absent as an ossified structure in adult skulls of some marsupials (e.g., *Monodelphis domestica*, Freyer, 1999; figs. 9 and 10). All the marsupial skulls I examined have at least an ossified caudal nasoturbinal, and in many marsupials both the rostral and caudal nasoturbinal elements are fused as a continuous bony structure (e.g., *Dasyurus hallucatus*).

The nasoturbinal is also referred to as *endoturbinal I* (Paulli, 1900a, 1900b, 1900c; Moore, 1981), the *nasal turbinal* in the pig (Parker, 1874), and *agger nasi* in human anatomy (Moore, 1981).

Ossified nasal septum: The nasal septum (septum nasi) is the midline structure that divides the nasal cavity into right and left chambers (e.g., figs. 5 and 6). The nasal septum is preformed in cartilage but the caudal two thirds of the septum is ossified in many

adult mammals (septum nasi osseum: NAV, 2005), a result of endochondral ossification. The ossification of the nasal septum in mammals proceeds from caudal to rostral, usually beginning ventral to the developing olfactory bulbs of the brain (Broom, 1926). In some mammals, ossification of the nasal septum proceeds rostrally from the presphenoid, but in other mammals ossification of the septum spreads from a more rostral and dorsal point, resulting in a separate mesethmoid bone (Broom, 1926, 1927, 1935). However, these interpretations, at least for some groups of mammals, warrant additional investigation (Ferigolo, 1981). There is some controversy in marsupials as to the origin of the ossified nasal septum. For example, the ossified septum in *Monodelphis domestica* is called the *presphenoid* by one group of authors (Clark and Smith, 1993) and the *mesethmoid* by another (Rowe et al., 2005). A separate mesethmoid ossification center indicating the presence of a mesethmoid is not documented for any species of marsupial. This has been examined in a small but diverse group of taxa (Broom, 1926; Clark and Smith, 1993). However, because the origin of the ossification of the nasal septum is not documented in most species of marsupials, I refer to this structure in adult specimens as the *ossified nasal septum*.

The ossified nasal septum is also frequently called the *perpendicular plate of the ethmoid* (e.g., Allen, 1882; Miller et al., 1964) or *lamina perpendicularis* (NAV, 2005) in the literature. However, the ossified septum is distinct from the ethmoid in embryology, derivation, and phylogeny (Rowe et al., 2005). The ossified nasal septum is derived from one or more midline endochondral ossification centers, either from the mesethmoid, the presphenoid, or both elements, whereas the ethmoid forms from several lateral perichondral ossification centers that arise in membranes induced by placodes (Rowe et al., 2005). The epithelium covering the ossified nasal septum is innervated by the terminal nerve (cranial nerve 0) in the embryos of a variety of mammals (e.g., Brown, 1987; Schwanzel-Fukuda et al., 1987; Witkin, 1987), whereas fibers of the olfactory nerve (cranial nerve I) innervate the epithelium surrounding the ethmoid. Finally, the ossified nasal septum and ethmoid are not present together in all mammals. For example, the ossified nasal septum and cranial nerve 0 are present in odontocete cetaceans, but the olfactory bulbs, ethmoid turbinals, and cribriform plate are absent in many of these taxa (Edinger, 1955; Ridgeway et al., 1987; Colbert et al., 2005).

Paraseptal shelf of vomer: The paraseptal shelf of the vomer is a lateral bony extension of the vomer that supports the vomeronasal organ in some marsupials such as *Monodelphis domestica* (fig. 34; Rowe et al., 2005). The paraseptal shelf of the vomer is continuous with the palatine process of the premaxilla rostrally, and caudally the paraseptal shelf fuses with the ethmoid plate to form the posterior transverse lamina (Rowe et al., 2005). The paraseptal shelf is informally called the *lateral wings of the vomer* (Negus, 1958), or the *wings of the vomer* (Maier, 2000).

Posterior transverse lamina: The posterior transverse lamina (*lamina transversalis posterior* in Voit, 1909; Freyer, 1999; Smith and Rossie, 2006; *lamina transversa* in NAV, 2005; *transverse lamina* in Rowe et al., 2005; *subethmoidal shelf* in Negus, 1958; Bhatnagar and Kallen, 1974b) is a sheet of bone whose rostral portion is formed by the caudal portions of the endoturbinals and its caudal portion by the vomer (Allen, 1882; Rowe et al., 2005; e.g., fig. 6). The portion of the posterior transverse lamina formed by the endoturbinals is the *ethmoid plate* (Rowe et al., 2005) and the portion formed by the paraseptal shelf of the vomer is called the *turbino-vomerine lamina* (Allen, 1882). The ventralmost ectoturbinal may sometimes contact the rostral portion of the posterior transverse lamina (fig. 22). The posterior transverse lamina forms the roof of the nasopharyngeal meatus (e.g., fig. 6). The posterior transverse lamina is distinct from the anterior transverse lamina (*lamina transversalis anterior*), which is a more rostral structure that supports the nasal cupula and the atrioturbinal, and does not ossify (Voit, 1909; Freyer, 1999; Maier, 2000).

Septoturbinal space: The space between the nasal septum and a particular turbinal element as it approaches the midline is the septoturbinal space (Allen, 1882). The septoturbinal space is called the *meatus nasi communis* or *common nasal meatus* in NAV (2005).

Sphenethmoid recess: The sphenethmoid recess (*olfactory recess* of Moore, 1981) is the bilateral space that is divided by the ossified nasal septum and occupied by the ethmoid bone and all associated turbinal structures (Rowe et al., 2005; e.g., fig. 6). The surfaces within this space are lined by either respiratory or olfactory epithelium (Rowe et al., 2005). The sphenethmoid recess comprises all the space within the nasal cavity except for the paired nasopharyngeal meatus. Caudally, the sphenethmoid recess is floored by the posterior transverse lamina and is roofed by the cribriform plate (Rowe et al., 2005). The caudalmost projection of the sphenethmoid recess into the orbitosphenoid and presphenoid is called the sphenoidal recess.

Sphenoidal recess: The sphenoidal recess (Negus, 1958) is the caudalmost projection of the sphenethmoid recess into the orbitosphenoid and presphenoid (fig. 31). The sphenoidal recess is roofed by the cribriform plate and is located caudal to endoturbinal IV. Endoturbinal V is housed in the sphenoidal recess of marsupials. This space is also called the *sphenoidal sinus* or *fossa* in the literature (e.g., Miller et al., 1964; Giannini et al., 2006; Sinus sphenoidalis in NAV, 2005).

Turbinal: A turbinal is any of the scrolled or curled projections into the nasal cavity; turbinals may be cartilaginous or bony. In this paper I focus on the bony turbinals including the maxilloturbinal, nasoturbinal, ectoturbinals, and endoturbinals, which

together comprise the ethmoid bone (fig. 5; Rowe et al., 2005).

The term *turbinal* is used here, coming from the Latin *turbinalia*. Others use *turbinate* (e.g., Miller et al., 1964) instead of *turbinal*; the latter term is used because it has priority (e.g., Allen, 1882) and it is more commonly used than the former term. The turbinals are sometimes referred to as the *lateral masses* of the ethmoid (e.g., Miller et al., 1964). Endoturbinals and ectoturbinals are also collectively called *olfactory plates* or *ethmoturbinals* (Ethmoturbinalia; NAV, 2005) in the literature (Allen, 1882; Paulli, 1900a, 1900b, 1900c; Moore, 1981).

Turbinal bifurcation: A turbinal bifurcation includes any branching or splitting point that occurs on the turbinal lamella and subsequent bifurcations of those branches (e.g., fig. 28). This term was informally used by Rowe et al. (2005). The products of a turbinal bifurcation are turbinal branches, a term used informally by Moore (1981).

Turbinal fold: A turbinal fold is a plication or scrolling of a turbinal element (e.g., fig. 20). The usage of the term *olfactory fold* by Allen (1882) is synonymous with the usage of turbinal fold in this paper. I apply the term *turbinal fold* to turbinals that have a respiratory function as well as those with olfactory functions.

Turbinal interspace: The turbinal interspace is the space between any two adjacent turbinal elements. The usage of the term *olfactory interspace* by Allen (1882) is synonymous with the usage of *turbinal interspace* in this paper. I apply the term *turbinal interspace* to turbinals that have a respiratory function as well as those with olfactory functions.

Turbinal lamella: The unbranched basal part of each turbinal element (Paulli, 1900a, 1900b, 1900c; Moore, 1981; e.g., fig. 28) by which it attaches to the nasal cavity wall (Allen, 1882). The original use of the term *lamella* was in association with only endoturbinals and ectoturbinals (Paulli, 1900a, 1900b, 1900c; Moore, 1981), but in this paper this term is used in reference to all turbinal elements. A synonym for *turbinal lamella* is *olfactory plate* (Paulli, 1900a, 1900b, 1900c; Moore, 1981).

Turbinal lobe: A freely projecting terminal end of a turbinal element (e.g., fig. 20). The term *olfactory lobe* was applied by Allen (1882) in reference to endoturbinals and ectoturbinals. I apply the term *turbinal lobe* to all turbinals, in recognition that some elements have a respiratory rather than olfactory function.

Uncinate process of nasoturbinal: The caudal nasoturbinal divides just rostral to the point of attachment of the lamella of endoturbinal I to the lateral wall of the nasal cavity (fig. 14). The uncinate process (Processus uncinatus; Voit, 1909; Freyer, 1999; NAV, 2005) is the ventrocaudal portion of the caudal nasoturbinal that remains attached to the lateral wall of the nasal cavity.

APPENDIX 2

CHARACTER LIST FROM THE INTERNAL NASAL SKELETON

1. Complexity of rostral maxilloturbinal: arborlike with many branches (0), or simple with a single scroll (e.g., *Monodelphis*, *Phascolarctos*), curled lamella (e.g., *Vombatus*), or only a single bifurcation (e.g., *Isoodon*, *Echymipera*, *Macrotis*, *Myrmecobius*, *Notoryctes*, *Tarsipes*) (1). This character was examined in the same coronal plane as the rostral portion of the root of the upper canines for taxa with canines. For those taxa without canines, this character was examined in the coronal plane immediately posterior to the caudalmost upper incisor. For *Vombatus*, this character was examined at the rostralmost extent of the maxilloturbinal because this taxon has only one upper incisor with an extensive root and no canines. Among the taxa examined here, there is a clear distinction between those exhibiting state (0) versus state (1). Taxa either had maxilloturbinals with many branches or a single branch, respectively; none showed an intermediate state (e.g., two, three, or a “few” bifurcations or scrolls of maxilloturbinal). This character is illustrated in figure 28.
2. Caudalmost portion of maxilloturbinal: simple in morphology with few branches and scrolls and is attached to nasal cavity wall or floor (0), or the caudalmost portion of the maxilloturbinal is an enclosed tube that tapers into a cone that is unattached to nasal cavity (1). This character is illustrated in figure 38.
3. Caudalmost attachment of maxilloturbinal: floor of nasal cavity (0), or lateral wall of nasal cavity (1). This character was assessed at the caudalmost point at which the maxilloturbinal is still attached to the nasal cavity. This character is illustrated in figure 32.
4. Maxilloturbinal contact with nasoturbinal: absent (0), or present (1). This character is illustrated in figure 33.
5. Rostral nasoturbinal as an ossified structure in adults: present (0), or absent (1). This character is illustrated in figure 9.
6. Rostral nasoturbinal morphology: well developed as a slender ventromedially directed process (0), or small, robust bony process with a ventromedial inflection (1). This character is illustrated in figure 10.
7. Caudal nasoturbinal morphology: unbranched (0), or has at least one branch (1). This character is illustrated in figure 12.
8. Caudal nasoturbinal pneumaticity: absent (0), or present (1). This character is illustrated in figure 35.
9. Shape of rostral portion of caudal nasoturbinal: rostradorsal and rostroventral portions are straight (without a kink) (0), or distinctive kink between rostradorsal and rostroventral portions of caudal nasoturbinal (1). In most of the taxa scored as having state (1) and having at least two upper premolars, the kink is located in the coronal slices just caudal to P2. However, in some taxa the kink is first noticeable in the same coronal slice as the C or P1. The kink occurs caudal to P4 in *Thylacinus*, even with M3 in *Vombatus*, and even with M4 in *Phascolarctos*. This character is illustrated in figure 11.

10. Caudodorsal portion of caudal nasoturbinal (caudal to nasoturbinal division around endoturbinal I): caudodorsal portion is unfolded (0), or caudodorsal portion curls (1). This character is illustrated in figure 13.
11. Uncinate process of nasoturbinal: present (0), or absent (1). The uncinate process is the caudoventral attachment of the caudal nasoturbinal that remains caudal to the division of the nasoturbinal around endoturbinal I. This character is illustrated in figure 14.
12. Caudalmost point of ventral attachment of caudal nasoturbinal: medial wall of lacrimal canal (0), lateral wall of nasal cavity (1), medial wall of infraorbital canal (V_2) (2), floor of nasal cavity (3), or maxilloturbinal (4). This character is illustrated in figure 15.
13. Caudalmost extent of ventral attachment of nasoturbinal: rostral to caudal terminus of maxilloturbinal (0), at coronal level of caudal terminus of maxilloturbinal (1), or caudal to caudal terminus of maxilloturbinal (2). This character is illustrated in figure 16.
14. Packing of endo- and ectoturbinals: relatively loosely packed (0), or complexly branching or convoluted elements that are densely packed creating a tight mazelike pattern, especially around the ossified nasal septum (1). This character was examined at the level at which all endoturbinals and ectoturbinals are visible in the same coronal slice. This slice is through the orbits and usually contains the following surrounding anatomical structures: zygomatic arch or rostral root of the arch, frontal bone roofing the nasal cavity, section through the penultimate or ultimate pair of upper and lower molars. This character is illustrated in figure 6.
15. Number of turbinal folds on endoturbinal I: none (0), one (1), two (2), or three (3). This character was examined at the level at which all endoturbinals and ectoturbinals are visible in the same coronal slice. This slice is through the orbits and usually contains the following surrounding anatomical structures: zygomatic arch or rostral root of the arch, frontal bone roofing the nasal cavity, section through the penultimate or ultimate pair of upper and lower molars. This character is illustrated in figure 20.
16. Rostral portion of endoturbinal I (part above the maxilloturbinal): present (0), or absent (1). This character is illustrated in figure 39.
17. Rostral portion of endoturbinal I: contains no pneumatic cavities (0), possesses a small pneumatic cavity, which encompasses only a portion of the coronal cross section of the element (1), or possesses a large cavity, which encompasses most of or the entire coronal cross section of the element (2). This character is illustrated in figure 19.
18. Number of endoturbinals: two (0), three (1), four (2), five (3), six (4), seven (5), or more than seven (6). *Tachyglossus*, an outgroup, is the only taxon examined in this study that has more than seven endoturbinals (18 total), and this is the justification for the wording of character state 18.6. This character is illustrated in figure 18.
19. Number of ectoturbinals: one (0), two (1), three (2), or four (3). This character is illustrated in figure 21.
20. Morphology of the ventralmost ectoturbinal: bifurcating (0), or does not bifurcate (1). This character was assessed near the rostralmost point of contribution of the ventralmost ectoturbinal to the cribriform plate. This character is illustrated in figure 41.
21. Ectoturbinal(s) is tubelike in shape: absent (0), or present (1). This character is illustrated in figure 40.
22. Rostral portion of ventralmost ectoturbinal: lamella does not contact posterior transverse lamina (0), or lamella is attached to posterior transverse lamina (1). This character is illustrated in figure 22.
23. Dorsoventral extent of caudal portion of lateral recess: recess does not extend to nasal cavity floor (0), or recess extends to nasal cavity floor (1). This character was assessed in the coronal slice through the caudalmost extent in which the medial wall (caudal nasoturbinal) of the recess is complete. This character is illustrated in figure 48.
24. Caudal extent of lateral recess: rostral in the snout, maxilloturbinal extends caudal to this (0), about even with the caudal terminus of the maxilloturbinal (1), or extends caudal to the maxilloturbinal (2). This character was assessed in the coronal slice through the caudalmost extent in which the medial wall (caudal nasoturbinal) of the recess is complete. This character is illustrated in figure 49.
25. Maxillary recess: present (0), or absent (1). The maxillary recess is the ventral portion of the lateral recess that is bounded dorsally by the lamella of endoturbinal I. This character is illustrated in figure 26.
26. Maxillary recess: caudal portion of recess is medially enclosed by posterior transverse lamina (0), or uncinate process of the caudal nasoturbinal also contributes to the medial wall of the recess (1). In state (0), the maxillary recess is confluent with the recessus glandularis (Freyer, 1999). This character is illustrated in figure 27.
27. Frontal sinus: no frontal sinus (0), small frontal sinus present (comprises less than half of the cross sectional area of the frontals) (1), or large frontal sinuses present (comprises most or all of the cross sectional area of the frontals) (2). This character is illustrated in figure 25.
28. Paraseptal shelf of vomer: present (0), or absent (1). This character was examined rostral to the vomerine contribution to the posterior transverse lamina. This character is illustrated in figure 34.
29. Rostral extent of ossified nasal septum: rostral to crowns of upper canines (0), even with crowns of upper canines (1), or caudal to crowns of upper canines (2). This character is illustrated in figure 29.
30. Ventral portion of ossified nasal septum: straight or only with slight bends or convolutions (0), or very convoluted (1). This character was examined in the nasal cavity rostral to the sphenoidal recess. This character is illustrated in figure 36.

31. Prominent lateral expanded bulges within the shaft of the ossified nasal septum: present (0), or absent (1). This character includes bulges anywhere along the length of the ossified nasal septum with the exception of the swelling at the base of the septum that appears to be ubiquitous among marsupials. This character is illustrated in figure 24.
32. Contribution of turbinal elements to the cribriform plate: all ecto- and endoturbinals contribute to the cribriform plate (0), or not all elements participate in the cribriform plate (1).
33. Contribution of posterior transverse lamina to the cribriform plate: absent (0), or present (1). This character is illustrated in figure 30.
34. Crista galli: present (0), or absent (1). This character is illustrated in figure 23.
35. Caudalmost portion of nasal cavity (sphenoidal recess) laterally restricted by the endocranial cavity: absent (0), or present (1). In state (1), the endocranial cavity surrounds the lateral walls of the sphenoidal recess at the caudal extent of the recess. This character is illustrated in figure 31.

